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ON THE GEOGRAPHIC DISTRIBUTION AND ECOLOGICAL RELATIONS OF THE BOG PLANT SOCIETIES OF NORTHERN NORTH AMERICA.

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(WITH THREE MAPS)

By the term "bog-plant societies," as used in this paper is meant that group of plant societies which is commonly found inhabiting undrained depressions and marshy grounds in the northern United States and Canada. In the northern states they have become noted for their possession of such anomalous plants as the sundew, pitcher-plant, tamarack, and cranberry. Although not so well known, the cassandra, rosemary, and Labrador tea are quite as interesting.

"DRAINED SWAMP" AND "UNDRAINED SWAMP" SOCIETIES.

There have been a number of descriptions of these bogs published in connection with local ecological studies, and in several instances have comparisons been made between them and the other swamps of the region. They are referred to as "undrained swamps," in contrast with the groups of "drained swamp" societies which may be found on adjoining low grounds and along stream courses. The latter group may be briefly summarized by noting that in the region under discussion it is commonly made up of such plants as Typha latifolia[1], Scirpus lacustris, Juncus effusus, Carex riparia, Polygonum emersum, P. sagittatum, Cephalanthus occidentalis, Cornus stolonifera, C. candidissima,

[1] Nomenclature of Britton's Manual of the Flora of the Northern States and Canada, 1901.

Salix discolor, Acer rubrum, Ulmus americana, and Fraxinus americana.

While it often happens that locally the one occurs only in drained conditions and the other only in undrained situations, field work carried on over any considerable area will show that drainage conditions are not adequate to account for the presence or absence of either of these two distinct types of vegetation. The presence of peat, with the consequent accumulation of humus acids, has been commonly spoken of as preventing the coming in of the "drained swamp" types. In southern Michigan and northern Indiana, however, there are many swamps with a thick substratum of peat and without an outlet, yet supporting a vegetation made up wholly or in part of these plants. It is true, however, that the bog societies occur here only in poorly drained situations, underlaid with peat or bogus soil.

Again, it is not unusual to find these two society groups growing on opposite sides of the same lake, where the underlying soil can be shown to be the same. To account for this, it has been suggested that the depth of water in the two situations is of importance. But any ideas of this kind can be disproved by carrying the criteria into a new locality. Just to the west of Ann Arbor, Mich., occurs a small glacial lake. This was formerly surrounded by a quite typical group of bog societies. Within recent years the eastern side of the lake has been entirely cleared, and a large part of the original tamaracks on the south and southwest sides have been cut away. There is left a rather pure growth of bog plants on the northwest side. Since the clearing was made on the southwest side there has sprung up a dense growth of herbs, shrubs, and trees, nearly equaling in height the adjoining grove of tamaracks. But if we note the species prevailing in this area, we find the plants enumerated above as typical of drained swamps. It is practically impossible to account for this situation on the basis of soil difference, chemical character of the soil solution, drainage conditions, or depth of water.

In his paper on the "Physiographic Ecology of Chicago and Vicinity" Cowles[2] distinguishes one "drained" and three

[2] BOT. GAZ. 31: 145–155.

"undrained" types of swamps occurring in the area of lakes and sand dunes at the southern end of Lake Michigan. Although several species of plants may be common to two or more, he does not believe these societies to be related to one another genetically.

That a certain amount of chance in the matter of seed dispersal must be taken into account in any botanical field problem is recognized. But the fact that "drained" and "undrained" swamps occur in close proximity to one another, each with numerous examples in the same district, seems to require some more adequate explanation.

RELATION TO SURROUNDING VEGETATION.

Throughout the region of northern Indiana, northern Ohio, and southern Michigan the problem is still further complicated by a seeming absence of all connection between the bog societies and the bordering forests. The zonal succession of plant groups, from the submerged aquatics of the pond to the arborescent forms of the higher bog margin, are clearly defined and well known. But then comes a sudden break, and without a suggestion of gradation the surrounding forest of mature oaks or oaks and hickories appears.

Farther north in Michigan there is no such difficulty in finding a definite order of succession between the bogs and forests surrounding them. For example, a tamarack swamp on north Manitou Island, which is surrounded by a thick forest of maple and beech, shows the following societies arranged almost zonally, beginning with the open pond in the center:

1. AQUATIC SOCIETY. Potamogeton natans, P. lucens, Nymphaea advena, Castalia odorata.

2. CAT-TAIL-DULICHIUM SOCIETY. Typha latifolia, Phragmites Phragmites, Menyanthes trifoliata, Dulichium arundinaceum, Cicuta bulbifera, Scheuchzeria palustris.

3. CASSANDRA SOCIETY. Chamaedaphne calyculata, Dryopteris Thelypteris, Sphagnum sp. ?, Kalmia glauca, Sarracenia purpurea, Ledum groenlandicum, Lycopus americanus, Triadenum virginicum, Polygonum Hydropiper, Rubus hispidus, Comarum palustre, Andromeda Polifolia, Chiogenes hispidula, Oxycoccus Oxycoccus, and Eriophorum virginicum.

4. SHRUB AND YOUNG TREE SOCIETY. Aronia arbutifolia, Ilicioides mucronata, Rosa caroliniana, Ilex verticillata; young specimens of Larix laricina, Betula pumila, Picea Mariana, and Acer rubrum. Beneath these occur a scattering of members of the preceding society, together with Limnorchis hyperborea, Blephariglottis lacera, Gymnandeniopsis clavellata, Osmunda regalis, O. cinnamomea, Dryopteris spinulosa intermedia, Vaccinium canadense, Epilobium lineare, E. adenocaulon, and Viola blanda.

5. CONIFER SOCIETY. This zone is composed of mature tamaracks, black spruces, low birch, and swamp maples; young and mature Betula lutea and Tsuga canadensis; and seeding Acer saccharum. The undergrowth of herbs and shrubs is diminished to a few stragglers. This brings us to the higher ground surrounding the bog, which is occupied by the next society.

6. CLIMAX FOREST SOCIETY. Consists of sugar maples and beech trees with occasional hemlocks. The undergrowth is sparse, consisting principally of their own seedlings.[3]

Going farther north into Ontario, the series of societies is not so long, but apparently just as definite. But we have there passed the northern limits of our broad-leaved mesophytic trees and the climax stage is reached in a mixed forest of pine, spruce, and fir. This same statement probably holds for the great coniferous areas of Wisconsin, Minnesota, New York, northern Pennsylvania, and the New England states. Even so far south as northern Indiana, in the sand-dune region, Cowles[4] has shown that where the surrounding vegetation consists of pines there is no doubt the same order of succession.

It appears then that where the northern conifers are dominant or make up an integral part of the forests, the ecological relations of the bog societies are clear. In other words, they normally represent one physiographic starting-point for the development of the great conifer forest formation.

There remain therefore at least two questions to be solved:

[3] See also WHITFORD, H. N., The genetic development of the forests of northern Michigan. BOT. GAZ. **31**: 315. 1901.

[4] *Loc. cit.*, p. 150.

First. What relation do these bog societies bear to the surrounding vegetation of oaks and hickories as they occur in Ohio, Indiana, and southern Michigan?

Second. How can we account for the presence of bog societies and swamp societies (or mixtures of the two) when found in adjacent areas, having similar drainage and soil conditions?

PRESENT DISTRIBUTION OF BOG PLANTS.

In order to obtain a better understanding of these questions, data on the geographic distribution of bog plants were collected and maps drawn. It soon became evident that the number of species would have to be limited and that only those which are characteristic of these situations across northern North America could be considered. The number was finally reduced to fifteen. Beginning with those which first find a foothold in such depressions and continuing in their approximate order of advent, they are: Menyanthes trifoliata, Dulichium arundinaceum, Comarum palustre, Scheuchzeria palustris, Eriophorum polystachyon, Drosera rotundifolia, Sarracenia purpurea, Oxycoccus Oxycoccus, Chiogenes hispidula, Andromeda Polifolia, Chamaedaphne calyculata, Ledum groenlandicum, Kalmia glauca, Betula pumila, and Larix laricina.

Finally the accompanying map (*fig. 1*) was drawn by superimposing the areas of North America in which each of these plants commonly occurs. In the course of its construction some interesting points in geographic distribution came to light. The dark area extending from the Atlantic to the Mackenzie basin represents a great center throughout which all these plants appear in most bogs. The lighter shaded areas north and south represent territory in which only a majority of the forms occur in the average bog, while in the lightest shaded portions only a minority of them are to be found.

CLIMATE OF THE OPTIMUM REGION.

The region of optimum distribution is limited by certain climatic barriers. On the southwest its limits coincide closely with those of the forests. Beyond this area the relation between rainfall and evaporation makes the conservation of water in

FIG. 1.—Map showing distribution of bog plants. (1) Drosera, Dulichium. (2) Sarracenia, Drosera, Dulichium, Eriophorum, Chiogenes, Chamaedaphne. (3) Dulichium, Menyanthes. (4) Drosera, Comarum, Menyanthes, Eriophorum, Ledum, Andromeda. (5) Drosera, Comarum, Menyanthes, Eriophorum, Oxycoccus, Andromeda, Ledum, Kalmia, Chamaedaphne. (6) Menyanthes, Oxycoccus, Ledum, Andromeda, Kalmia. The presence of a large number of shrubs in Alaska and Greenland is probably connected with their preservation there during glacial times.

depressions throughout the year impossible. On the south and southeast, while the rainfall and relative humidity are favorable, the intense insolation of the summer months seems to be the controlling factor. The northern boundary coincides with that of the northern limits of dense forests. According to Kjellman,[5] Kihlman[6] and Warming,[7] this boundary is controlled by the amount of snowfall, exposure to dry winter winds, and the length of the growing season. There does not appear to be any relation between the distribution of this group of plant societies and the "life zones" distinguished by Merriam.[8] Within the belt of optimum conditions the climate is characterized by great range of temperature, both daily and annual. As we go toward the east from the Mackenzie basin, this is modified by the increase in relative humidity. The summers are short, bright, and warm, with abundant rainfall, principally in the form of thunder showers. The winters are long, and extremely low temperatures may occur. The snowfall increases from a foot or two in the western part to several feet in Ontario and the St. Lawrence basin. In the Northwest Territories, where the tundra vegetation is dominant, the ground below a depth of a few centimeters is frozen practically throughout the year. Since air temperatures of 21° C. are common in late spring and summer, the plant roots and shoots must there withstand remarkable temperature differences. With the exception of the eastern maritime provinces and Maine, no part of this optimum area is comparable with the conditions which call forth the great bog development of northern Germany and Scandinavia. In the latter localities the bogs are confined to depressions, but may occur in a variety of topographic situations. They may even invade established forests, and by raising the ground water level destroy the tree covering.[9]

[5] KJELLMAN, F. K., Aus dem Leben der Polarpflanzen. Leipzig. 1883.

[6] KIHLMAN, A. O., Pflanzenbiologische Studien aus Russisch-Lappland. Acta Soc. pro Fauna et Flora Fennica **6**. 1890.

[7] WARMING, E., Ueber Grönlands Vegetation. Engler's Botan. Jahrbücher **10**. 1888.

[8] MERRIAM, C. H., Life zones and crop zones of the United States. Bull. 10, U. S. Dept. Agric. 1898.

[9] GANONG, W. F., Raised peat bogs in the province of New Brunswick. Proc. Roy. Soc. Can. II. **3**[4]: 131–163. 1897.

It is also worthy of note that in the southeastern part of this region the bog flora is increased in variety by a large number of plants whose range is more southerly than that of the typical bog plants. Among these are Vaccinum corymbosum, V. atrococcum, Rhodora canadensis, Aronia arbutifolia, and Viburnum cassinoides. Their distribution points to a northward migration from the southern Appalachians.[10]

VARIATIONS OF THE BOG FLORA IN GEOGRAPHIC RANGE.

But the map has a still greater significance. The dark area represents the region in which most of these plants attain their highest physical development. Those who have seen the magnificent groves of tamarack in the north, attaining a height of thirty meters and a bole diameter of a meter, will appreciate this fact when they compare them with the stunted groups of the larch in the bogs near the southern and northern limits.

Again, within this same belt, at least eight of the plants, the buckbean, cranberry, snowberry, rosemary, leather leaf, labrador tea, birch, and tamarack, are not confined to bog areas. They may be said to have there a wider life-range and are to be found in a variety of habitats. The tamarack, for example, is found on the hills and along most of the streams. With the black and and white spruce and pine, it makes up a large part of the forest. Here too the buckbean, leather leaf, Labrador tea, and birch occur along slow streams, and the rosemary, snowberry, and cranberry in moist ravines and rich woods.

Just as striking, perhaps, is the fact that as we go in any direction away from this optimum region, the first plants to diminish in size and frequency of occurrence are the arborescent tamarack and birch. Then follow in close succession the shrubby forms, and finally the herbaceous species.[11] This is practically a reversal of the order of their coming into a new area, and, as we shall see later on, this may have some connection with the

[10] ADAMS, C. C., Southeastern United States as a center of geographical distribution of flora and fauna. Biol. Bull. 3:123. 1903.

[11] *Scheuchzeria palustris* is an exception, so far as its eastern distribution is concerned, and has about the same range as *Betula pumila*, but in the west it reaches its southern limit in Colorado and California.

migration this vast aggregate of bog societies has made since the glacial period. It also represents an order from the tallest forms to those raised but slightly above the wet substratum.

PREGLACIAL DISTRIBUTION.

Of these fifteen species, three, Dulichium, Sarracenia, and Kalmia, are endemic. The larch and birch are represented in the Old World by closely related forms, while the remaining ten occur in similar habitats in Europe and Asia. This naturally points to their origin, and certainly indicates their preglacial distribution to have been in the circumpolar regions of both continents. It also implies that these great land masses must have been connected for a long time during the Tertiary period, so that migration from one to the other was by no means difficult. Whether these forms originated in a single polar area is of little consequence. They may have arisen partly in America, partly in Eurasia, but they were essentially the products of similar conditions and by migration came to be associated.

THE GLACIAL MIGRATIONS.

With the coming on of the cold period, which closed the Tertiary and inaugurated such extremes of climate between the equator and the poles, the consequent accumulation of ice on these northern continents destroyed the ancient habits of these plant societies. At the same time semitropical species, which were common alike to high and low latitudes, were killed by the increasing cold, the ground they had covered affording new areas for occupancy. By the reversal of the drainage lines and consequent destruction of low-ground vegetation, new habitats suited to these plants arose in advance of the ice invasion. Just as the zones of vegetation in a small lake move toward the center, because that is the only direction in which development is possible, so these plants spread away from the centers of ice accumulation. Where this migration moved to the west the plants were later on destroyed, but their southward extension brought them into areas which were not within reach of the subsequent ice invasion. Their adaptations for rapid seed dispersal are not

notable, except in the case of the Dulichium and cottongrass. The larch and birch have winged seeds, while the remainder would seem to be dependent upon transportation by birds and water currents. But the fact that the plants have survived the ice advances proves that they were easily able to establish themselves in new areas as rapidly as the climate changed. Not less than five such geographic migrations of more or less latitude, corresponding with the five glacial epochs, must have occurred. Between them were intervals when the temperature, as shown by plant and animal remains[12] found in interglacial deposits, was fully as high as at the present time. If we consider this proved, then the only glaciation which could materially affect the distribution of our boreal societies today is that of the last or Wisconsin epoch. Through the work of Chamberlin,[13] Leverett,[14] Salisbury,[15] Upham,[16] and others, the limits of this ice invasion have been definitely mapped.

In order to get an idea of the distribution of the boreal plant societies during the maximum glaciation, let us try to picture what would become of these same societies if a similar period of glaciation were to come upon them now. A sufficient time has probably intervened since the last glacial epoch to allow of almost perfect climatic adjustment on the part of the tundra and conifer societies, so that the climate now most favorable for their development may well have characterized a zone just beyond the ice margin. This zone would gradually move with the increase of the ice fields until it would come to occupy the position shown in *fig. 2*. According to Chamberlin, the climatic conditions pre-

[12] COLEMAN, A. P., Glacial and interglacial beds near Toronto, Jour. Geol. **9**: 285. 1901. PENHALLOW, D. P., The Pleistocene flora of the Don Valley. Rept. Brit. Ass. Adv. Sci. **1900**: 334.

[13] CHAMBERLIN, T. C., Classification of American glacial deposits. Jour. Geol. **8**: 270; The glacial phenomena of North America, Geikie's *Ice Age*, 3d ed. p. 274. 1894.

[14] LEVERETT, F., Changes of climate indicated by interglacial beds. Proc. Bost. Soc. Nat. Hist. **24**: 455. 1890.—The Illinois glacial lobe. Mon. 38, U. S. G. S.—The glacial formations and drainage features of the Erie and Ohio Basins. Mon. 41, U. S. G. S.

[15] SALISBURY, R. D., and ATWOOD, W. W., The geography of the region about Devils Lake and the Dalles of the Wisconsin. Bull. 5, Wis. Geol. and Nat. Hist. Sur. SALISBURY, R. D., Glacial geology of New Jersey. Rep. State Geologist N. J. **5**. 1902.

[16] UPHAM, W., The Glacial Lake Agassiz. Mon. 25. U. S. G. S. 1896.

FIG. 2.— Map showing hypothetical distribution of forests and tundra during maximum glaciation of the Wisconsin Epoch.

vailing about the margin were intermediate between those of Greenland and Alaska at the present time. In the former case the vegetation is sparse and of tundra type, in the latter the forests occur on the stagnant ice margin.[17] It would appear then that the glaciers would not affect the tree distribution at any great distance from the ice front. But there are other factors which would affect the breadth of the zone of conifer dominance. As we may learn from their present distribution, a dry climate, a youthful topography in which erosion is active, high elevation and sterile soil, all of which imply great variations in temperature and relative humidity, are more favorable to conifers than to broad-leaved deciduous trees.

It should also be noted in connection with the development of the continental glacier that, as the ice sheets spread from the two great centers of accumulation, they unite in the region north of lakes Superior and Huron. With their near approach to the lakes, the area of conifers is divided into an eastern and western section. As the development proceeds toward the Wisconsin terminal moraine, the western section would be forced toward the Great Plains, while the eastern division would spread south to the Appalachian highlands and coastal plain.

But in the interior the Ohio basin was occupied by the oaks, ash, hickories, elms and maples. Judging by the present northern limits[18] of some of these species it is doubtful if the conifers could compete with them at any great distance from the ice front, so that the belt of tundra and conifers may have extended as far south as the Ohio, but it seems probable that even north of this river species of oak, ash elm, and maple persisted.

DISTRIBUTION DURING MAXIMUM GLACIATION.

To be more definite, let us briefly note the conditions that would prevail during the time of maximum extension, from the Atlantic to the Rockies. In New Jersey, with its extensive area of sand and slow-flowing streams, conditions must have been

[17] RUSSELL, I. C., Glaciers of North America. Ginn & Co. 1901.

[18] BELL, R., The geographical distribution of forest trees in Canada. Scot. Geog. Mag. 13: 281. 1897.

favorable for a wide-spreading zone of boreal societies. In Pennsylvania the high relief of the Appalachians and consequent low temperature also afforded exceptional opportunities for the spread of these societies far to the south. Here too the cold water of the glacial drainage pouring down the numerous tributaries of the Allegheny, Susquehanna, and Delaware rivers may have had a marked influence by lowering the temperatures of the narrow valleys, just as the streams which flow from Mount Katahdin and the glaciers of Mount Hood (Cowles) and Mount Shasta (Merriam)[19] affect the temperature of their adjacent valleys today. The presence of many such northern forms as the white pine, spruce, and hemlock in areas of the southern Appalachians has long been attributed to the glacial period.[20] In the Ohio valley the streams flowing from the south would aid in maintaining equable temperatures and preserving the broad-leaved mesophytes as far north as the Ohio River. Beyond the Mississippi the conditions must have resembled those now prevalent in the Saskatchewan basin. Bessey[21] reports the occurrence in Nebraska of deposits of "well defined branches, twigs and occasionally tree trunks" at depths varying from twenty to fifty feet below the surface, and concludes that in recent geological times there must have been extensive conifer forests throughout the state. The present distribution of trees in Nebraska shows outliers of the western yellow pine (*Pinus ponderosa scopulorum*) in the central part of the state far removed from the main area of its occurrenee.

Now as to the bog plants: since under favorable conditions they may occupy other habitats than undrained depressions, they probably existed on the borders of the heavily loaded streams, in ravines and moist situations generally along the whole ice front. It is to be noted that practically all of the

[19] MERRIAM, C. H., Results of a biological survey of Mt. Shasta, California. North Americana Fauna no. 16. 1899.

[20] GRAY, A., Forest geography and archaeology. Amer. Journ. Sci. and Arts III. **16**:85. 1878. HOOKER, J. B., The distribution of North American flora. Amer. Nat. **13**:155. 1879.

[21] BESSEY, C. E., The forests and forest trees of Nebraska. Ann. Rep. Neb. State Bd. of Agri. **1888**:93.

existing small lake areas of the northern states were covered by the ice during the maximum extension of the Wisconsin ice sheet. As there is no reason to believe that the drift sheets of the preceding epochs, which in many places extend beyond the Wisconsin terminal moraine, contained such small undrained depressions, it follows that the bog societies must have occupied other habitats.

POSTGLACIAL NORTHWARD MIGRATION.

With the renewal of a milder climate and the consequent recession of the glaciers, the plant societies would gradually spread in the direction of continuous habitats and generally northward. The bog and tundra types would be the first to push into the barren ground left by the retreating ice. The area over which they spread in early postglacial times must have been very much more extensive even than that now occupied by them. In the smaller glacial depressions where absence of wave action would favor littoral vegetation, the bog plants would become firmly established. On the western and eastern sides of the glaciated area the tundra would be closely followed by the conifer forests.

In the west the spreading of the conifers to the north was followed by their gradual destruction in the southwest, due to the increase in temperature as compared with the rainfall. It is possible that the rainfall in Nebraska was never any greater than at the present time. But the decrease in transpiration accompanying decrease in temperature might account for the presence there during glacial times of trees which cannot live under present conditions. The bog plants perished with the conifers and their southwestern boundaries today correspond with that of the forest.

In the east, among the highlands, exceptional circumstances were afforded for the preservation of these northern forms. Many relicts still crowd the higher elevations as far south as western North Carolina.

But in the northern Ohio valley, with its scant conifer vegetation, the areas which at that time supported the bog societies

were encompassed by broad-leaved forests. The oaks, hickories, maples, ash, and elm, following the lines of their specific habitat, the stream valleys or uplands, the sandy stretches left by glacial drainage, or the long lines of clay moraines, surrounded them in their northward progression.

Probably if the pines, spruce, and hemlock had ever been dominant in Ohio, Indiana, and southern Michigan we should find some evidences of their former occupation by way of isolated conifer areas. Excepting the southern and eastern shore of Lake Michigan and two small groups of pines in Ingham and Calhoun counties, Michigan, no conifer areas occur south of the Grand and Huron River valleys. When the early settlers moved into the region of southern Michigan, its forests were of the type commonly known as "oak openings." Probably no type of broad-leaved forest would be more favorable for the preservation of conifer areas had they been dominant for any great length of time after the ice retreat. Where they have been planted within this region, they flourish and attain their normal proportions. Judging by the present distribution of *Pinus Strobus* and *Pinus resinosa*, the character of the soil in the vicinity of lakes Michigan, Huron, and Erie, and the meteorological conditions associated with these lakes, it seems probable that the conifers have reached their present distribution in the lower peninsula of Michigan by way of the lake shores. Probably the great bulk came by way of the southern end of Lake Michigan and from Ontario.

In the west, the north, and the east, then, the xerophytic bog societies are still found with their natural associates, the conifers (*fig. 3*). But in the Ohio valley they have been surrounded by a vegetation which bears no direct relation to them. Naturally, therefore, we should not expect to find an order of succession between them. This seems to be the answer to the first question proposed.

RELATION OF BOG SOCIETIES TO THE SWAMP SOCIETIES.

This also gives us a new basis for answering the second question, as to the presence of the bog societies and swamp societies

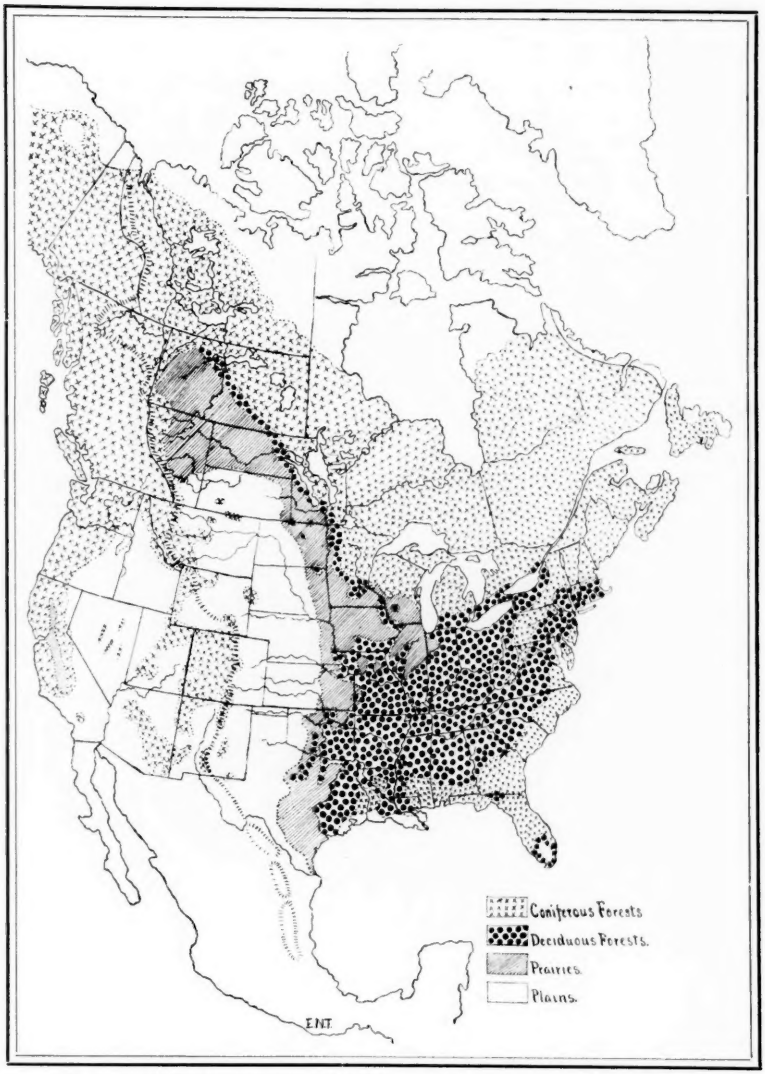


FIG. 3.— Map showing present distribution of forest, prairie and plains. (After Sargent, 10th Census, Vol. 9.)

in adjacent areas. As we know from the numerous physiographic studies that have been made of glacial basins, many of the lakes were formerly much larger than at present. Some of them in early postglacial times had steep banks, which were unfavorable to the development of shore vegetation. But by the lowering of the water level consequent upon the cutting down of the outlet, the shore line at present is a gradually sloping one, and supports a "drained swamp" flora. In other cases irregular arms, extending away from the main body of the lake and protected from wind and wave action, doubtless supported a bog vegetation during the tundra dominance. Since then they have been separated from the main lake by a lowering of the water level. Today we find in many such cases the bog vegetation still persisting in the depressions which were formerly arms of the lake, while on the shore of the main body, which came to be swampy at a much later period, the so-called "drained swamp" flora occurs. One of the best examples of this is Turkey Lake, Indiana. Here is an irregular lake several square miles in extent, nearly surrounded by high moraines. At its southeastern end, through a less elevated portion of the moraine, it formerly connected with several shallow depressions,[22] all of which contain bog plants with varying proportions of swamp plants. But on the now shallow margins of the present lake only the swamp plants are found. At Eagle Lake[23] the same observations hold for a former extension of this lake toward the northwest. But without multiplying examples, the relation of these two groups of swamp societies seems to depend largely upon the time when the swamps came into existence as swamp habitats. If they have existed since the days of tundra conditions they may show a bog flora today. If they are of recent origin, the plants will correspond to the normal swamp plants of the present climatic conditions. If of intermediate age, we may have various mixtures of the two. Dr. Cowles informs me that the only bog in the sand-dune region near Chicago which contains all these typical bog plants is the one that occurs on the Valpa-

[22] For map and description of lake see Proc. Ind. Acad. Sci. 1895.

[23] Map opposite p. 118, Proc. Ind. Acad. Sci. 1901.

raiso moraine. When this basin was formed the area occupied by the other bogs was still covered by the waters of Lake Chicago (now Michigan). At the present time new bog areas are being continually added by the interference of the moving dunes with drainage lines. And these new areas frequently contain a number of the bog plants. This, however, does not invalidate the explanation here suggested. The bog habitat has been continuous since early postglacial times; only its position and extent have been variable.

This same observation holds in the case of certain lakes which have long supported a growth of the bog plants at some part of their shore line. By recent gradual changes of level, or by the development of a floating sedge and cassandra zone, these areas have been greatly enlarged in recent times. Usually, however, such formations are partially made up of swamp species.

It is a well-known fact that in many localities where the bog societies formerly existed, they have partially or entirely disappeared. Since the settlement of this region, extensive bog areas have been cleared and drained. Fires have aided in the destruction of the tamaracks, and in many places the sudden lowering of the water level due to ditching has resulted in the killing of a large part of the original bog flora.

In this connection it is to be noted that the partial clearing or burning of a swamp area opens up a new territory for occupation, either by the bog plants or the swamp plants. The preservation of the underground stems of many of the bog species makes their chances more favorable for capturing the area in question. But there are many areas to the west of Ann Arbor which show that these bog plants cannot compete with the swamp plants in the occupancy of new territory, even though the bog plants be in complete possession previous to the clearing. We may say that the chances of capturing newly exposed land areas at the present time are all in favor of the swamp plants, largely because of their greater production of seeds, more adequate means for seed dispersal and better adaptations to present climatic conditions. In early postglacial times, however, the conditions were far different. The swamp plants had been

driven further south. The climate being more boreal in its character favored the bog plants, so that they became practically the only competitors for the low-ground situations.

The preservation of the bog societies in poorly drained situations down to the present time seems to be due (1) to the lower temperatures prevailing there, (2) to the sterile nature of the substratum, (3) to the completeness with which the substratum is occupied by the bog plants, and (4) to the fact that most bog habitats are associated with lakes, whose basins must be entirely filled with débris, before the drainage conditions will be naturally improved and made more favorable for the coming in of other plant societies.

To account for the xerophytic character of many of the bog plants, experiments now being carried on seem to indicate that differences of temperature between substratum and air is adequate. But the presence in many of our bog habitats of swamp species which show no xerophytic adaptations suggests that such xerophytic structures may be unnecessary under present conditions in *this* region.

SUMMARY.

To summarize the results of this study, we may say that, as shown by their geographic distribution:

1. The bog societies are typical of the colder portions of North America and are closely related to the bog societies of Europe and Asia.

2. They show an optimum region of dispersal having a moist climate, subject to very great temperature extremes. Within this region the plants have a greater range of habitats and an increased physical development.

3. As we go away from this center, either north or south, the first forms to show the effect of climatic change in diminished size and frequency of occurrence are the arborescent species. The species which extend furthest from this optimum region are herbaceous forms.

4. The bog societies are normally related to the conifer forests in their development to a climax tree vegetation.

5. Where surrounded by oaks and hickories, or in general

when conifers are absent, they show no order of succession to the forest societies. This is to be explained on the basis of the migrations forced upon all boreal societies during glacial times.

6. The absence of conifers in the Ohio basin probably indicates the dominance of broad leaved forms there during glacial times.

Local lake and bog studies seem to indicate that:

1. Present bog habitats are continuations of similar habitats which existed in early postglacial times, when tundra conditions and tundra vegetation were dominant.

2. The temperature phenomena of undrained depressions, containing deposits of peat, are favorable to the preservation of these types.

3. The "drained swamp" and "undrained swamp" classification will not hold over any great area. Undrained and drained depressions are both favorable to the development of the common swamp plants.

4. The bog societies are composed of boreal species and, in so far as the area of Ohio, Indiana, and southern Michigan is concerned, must be considered as relicts of former climatic conditions. The swamp societies, made up of more southerly forms, must be considered as the normal hydrophytic vegetation of the present climatic conditions.

The above results are put forth preliminary to a more detailed account to be published later. It is hoped that by this publication the author may be enabled to secure further data as to bog societies in other localities.

UNIVERSITY OF MICHIGAN.

ARALIA IN AMERICAN PALEOBOTANY.

EDWARD W. BERRY.

IN a study of the mid-Cretaceous floras of the Atlantic coastal plain, the difficulty of determining by what characters certain leaves were allied to Aralia, Sassafras, or Sterculia led to a somewhat extended review of these genera, more particularly the former, which is so abundantly represented throughout the American Cretaceous and Tertiary.

As to the relationship of these leaves with modern species of Aralia, we are not here especially concerned. Leaves of this type, however, are such a constant feature of these ancient floras, both in this country and abroad, that they possess an unusual degree of interest, and I have endeavored in the following notes to define more precisely the characters which serve to distinguish these leaves from leaves of other genera with which they are often confused.

The existing species of Araliaceae number about 450, which Harms, in *Die natürlichen Pflanzenfamilien*, distributes among 51 genera. They are widely distributed in the temperate and tropical regions throughout the world, and include herbs, shrubs, and trees with simple, lobed, or compound leaves. The genus Aralia, as restricted, includes some 27 species of North America and Asia with ternately and pinnately decompound leaves. The only fossil form which seems to stand in this ancestral line is *Aralia triloba* Newb. from the Fort Union Tertiary.

In North America north of Mexico we have six existing species of Aralia, four eastern and two western (besides three varieties). Of these *Aralia spinosa* L. is the only arborescent form. Beside Aralia two other genera occur with us: Panax, with two eastern North American species and five species of central and eastern Asia; and Echinopanax, with one species on the Pacific coast of America, which reappears in Japan. Many other genera occur in the West Indies, Mexico, Central and South America.

The fossil species throughout the world have mostly been referred to Aralia or Hedera, and are comparable for the most part with the existing species of the Araliaceae as a whole, rather than with these respective genera. Beside these two genera, various fruits from the Atane and Patoot beds of Greenland, and from the Miocene of Europe, have been referred to Panax; Unger identifies a species of Cussonia from the Miocene (Kumi) of Greece, Velenvosky another from the Cenomanian of Bohemia, and Nathorst a species of Acanthopanax from the Pliocene of Japan. Some 44 species of Aralia leaves have been identified from American strata, ranging from the Potomac formation upward through the Miocene. Numerous analogues of these American species have been described in Europe, as well as five species which are identical. Thus *Aralia coriacea* Velen., occurs in the Cenomanian of Bohemia and at Marthas Vineyard; *Aralia transversinervia* Sap. & Mar. occurs at Gelinden and has been reported from Long Island; *Aralia formosa* Heer occurs at Moletein and in the Bohemian Cretaceous as well as in the Dakota group and Raritan formation; *Aralia Zaddachi* Heer of the Baltic Oligocene occurs in the Californian Miocene; and *Aralia Looziana* Sap. & Mar. of the Gelinden flora reappears in the Fort Union group.

The genus is well represented both in the Cretaceous and Tertiary of Europe, Schimper in his *Paléontologie Végétale* (1874) listing 34 species, mostly, from European localities.

Heer describes two species from the Tertiary of Siberia, a simple leaflet and a lobed leaf of the *A. Saportana* type; while Ettingshausen notes the occurrence of Aralia in the Tertiary of Australasia. Many of these fossil species have merely a paleobotanical value. Thus Newberry identifies seven species at the single Raritan horizon of Woodbridge, N. J., four of which are described for the first time by him.[1] Still another Raritan species is Heer's *Aralia formosa*, which occurs in the upper layers at South Amboy, N. J. It is quite possible that Newberry's *A. polymorpha*, *groenlandica*, *patens*, *palmata*, and *rotundiloba* are all the varied leaves of a single species. In the Matawan formation,

[1] Flora of the Amboy clays. 1896.

which overlies the Raritan and with which it is closely related both geologically and botanically, there occur numerous Aralia-like leaves. I have identified[2] five species from this horizon, and the protean character of all of these mid-Cretaceous forms is emphasized when we find but two of these Matawan leaves referable to Raritan forms and these not entirely identical, while two others are entirely new.

Saporta would consider all the forms referred to Sassafras (Araliopsis) as included in the Araliaceae, but it seems to me that most of these leaves have stronger affinities in other directions. Ward would consider these Aralia-like leaves as referable to Platanus or its ancestral prototype. I have provisionally referred *Sassafras acutilobum* L. to Aralia.[3] Among the remainder of the American species of Sassafras, those which are not true species of Sassafras are related to Cissites or Platanus (Protoplatanus).

Three types of leaves have been referred to Aralia: (1) palmately three to seven-lobed leaves; (2) pinnately or ternately parted leaves; (3) simple leaves or leaflets.

Leaves of the first style, which concern us more particularly, may be briefly characterized as follows: Palmately 3–7 lobed, thick or coriaceous; petiole usually present and stout; margins entire or dentate; primaries 3–5 (7 in *A. dissecta*) generally rather stout, basal in ten species, sub-basal in ten species, and supra-basilar in fifteen species, doubtful in a few cases; lateral primaries when forked usually above their base, often present as basal sub-primaries; secondaries camptodrome in the entire-margined forms and craspedodrome in those which have dentate margins, both characters combined in some species; areolation obsolete, or square, or polygonal; base decurrent or cuneate in twenty species, rounded or truncate in fourteen species, doubtful in the balance, of which one is cordate and two or three are lobate. Young leaves may be entire-margined and three-lobed, while older leaves are dentate and five-lobed, which has caused a further duplication of species.

We may distinguish Sassafras, Sterculia, and Platanus,

[2] Flora Matawan formation. 1903. [3] BOT. GAZ. **34**: 438. 1902.

which are oftenest confounded with Aralia, by the following characters:

In *Sassafras* the primaries branch from the midrib, usually a considerable distance above the base, which is decurrent and never lobate; the margins are entire; the texture is not coriaceous; sinuses margined, or secondaries at least showing some evidence of disarrangement in the region of the sinuses; secondaries camptodrome; the decurrent base usually margined.

Sterculia has usually petiolate coriaceous leaves with obsolete venation and conically pointed lobes; is palmately lobed, usually from below the middle; primaries usually three from the top of the petiole; base cuneate; margins always entire; secondaries becoming effaced near the margin, or bowed close to the margin.

In *Platanus* the leaves are large, thick, and palmately lobed, not deeply so, however, and the sinus always open; coarse leaves three-nerved from near the base; primaries and secondaries straight and stout; secondaries numerous, parallel, usually craspedodrome; margin never entire; lobes always broad; base sometimes lobate.

The American species of palmately lobed Aralias may be separated into five groups.

SECTION 1.

Thick leaves fan-shaped in outline with long thick petioles; young leaves three-lobed; old leaves five-lobed; lobes narrow and pointed; base decurrent (except *A. Zaddachi*); sinuses narrow, extending more than half way to the base; margins dentate above with craspedrome secondaries, entire below with camptodrome secondaries; primaries three, stout, supra-basilar (except *A. Zaddachi*); lateral primaries forking some distance from the midrib; secondaries numerous and parallel. *Aralia digitata* Ward leads the way to the Green River species, *A. macrophylla* Newb., and by its lobate basal expansion shows its close relation to *Platanus basilobata* Ward.

This section includes: A. Saportana Lx., Dakota group; A. Saportana deformata Lx., Dakota group; Aralia sp., Dawson, Mill Creek; A. Welling-

toniana Lx., Dakota Tuscaloosa, and Raritan; A. digitata Ward, Fort Union group; A. Zaddachi ? Heer, Miocene.

SECTION 2.

Thick leaves rather orbicular in outline, with a long petiole (so far as it is known), lobes 3 to 5, broad and obtusely pointed, showing a tendency to become sub-lobate; base but slightly decurrent, generally rounded or truncate; sinuses open, extending about half way to the base; margins entire; secondaries camptodrome; primaries three, basal or sub-basal; lateral primaries unbranched, usually with sub-primaries below; areolation usually obsolete; smaller leaves than in section 1. A common type of mid-Cretaceous leaf is that which has been referred to *Aralia groenlandica* Heer and which has been recorded from the more or less synchronous strata of the Atane schists, the Dakota group, the New Jersey Raritan and Matawan formations, and the Island Raritan. I take as typical leaves of this species Heer's *f. 3. pl. 38* Fl. Foss. Arct. **6**, abth. 2 and Lesquereux's *f. 1, pl. 54*, Fl. Dak. Gr.; and it may be noted that Heer includes leaves which are considerably removed from this type, while Lesquereux includes Dakota leaves (*fig. 2, loc. cit.*) which approach on the one hand his *Aralia subemarginata* and on the other (*fig. 3, loc. cit.*) leaves which approach the synthetic group of Aralias which Newberry describes from the Raritan formation of New Jersey. This *groenlandica* type of leaf seems to be a rather primitive one, a leaf from which numerous rather closely related species have been derived.

This section includes: Aralia groenlandica Heer, Atane, Dakota, Raritan, Matawan, Island; A. gracilis Lx., Laramie ?; A. notata Lx., Denver and Fort Union; A. patens, Newb., Raritan, Island; A. rotundiloba Newb., Raritan and Island; A. polymorpha Newb., Raritan; A. palmata Newb., Raritan and Matawan; A. subemarginata Lx., Dakota; A. Brittonianum Berry, Matawan; A. acerifolia Lx., Ft. Union and Miocene.

SECTION 3.

Mostly large, very coriaceous, fan-like leaves, with very stout petioles and primaries; lobes 3 to 5 or more (?); the lobes long and rather slender (except *A. Ravniana*), obtusely pointed; sinuses narrow, primary ones deep, extending nearly to the base; base

decurrent; margins entire; secondaries (when preserved) numerous, parallel, and camptodrome; primaries three, basal or sub-basal; the lateral primaries forking some distance above their base; areolation generally obsolete; the small basal sub-primaries of section 2 wanting. The extreme of form in this section approach very close to the *Saportana* type of leaf of section 1.

The species included in this section are: Aralia Ravniana Heer, Atane and Matawan; A. Towneri Lx., Dakota and Matawan; A. quinquepartita Lx., Dakota and Raritan; A concreta Lx., Dakota; A. angustiloba Lx., Miocene; A. Wellingtoniana Vaughanii Kn., Woodbine, Dakota; A Jorgenseni Heer, Greenland Tertiary.

SECTION 4.

This and section 5 are residuary groups of species that require further study. This section includes a rather heterogeneous assemblage of fan-shaped leaves which agree in having entire margins; pointed lobes; usually stout primaries; petiole (where preserved) stout; primaries basal or sub-basal; texture coriaceous or sub-coriaceous; secondaries camptodrome (where known). Medium sized or small leaves except *A. Whitneyi*, which is very large and seems to be the Miocene ancestor of the existing Tetrapanax of eastern Asia.

The species included are: Aralia Masoni Lx., Dakota; A. Mattewanensis Berry, Matawan; A. Westoni Daws., Mill Creek; A. rotundata Daws., Mill Creek; A. radiata Lx., Dakota; A. tenuinervis Lx., Dakota; A. Whitneyi Lx., Miocene.

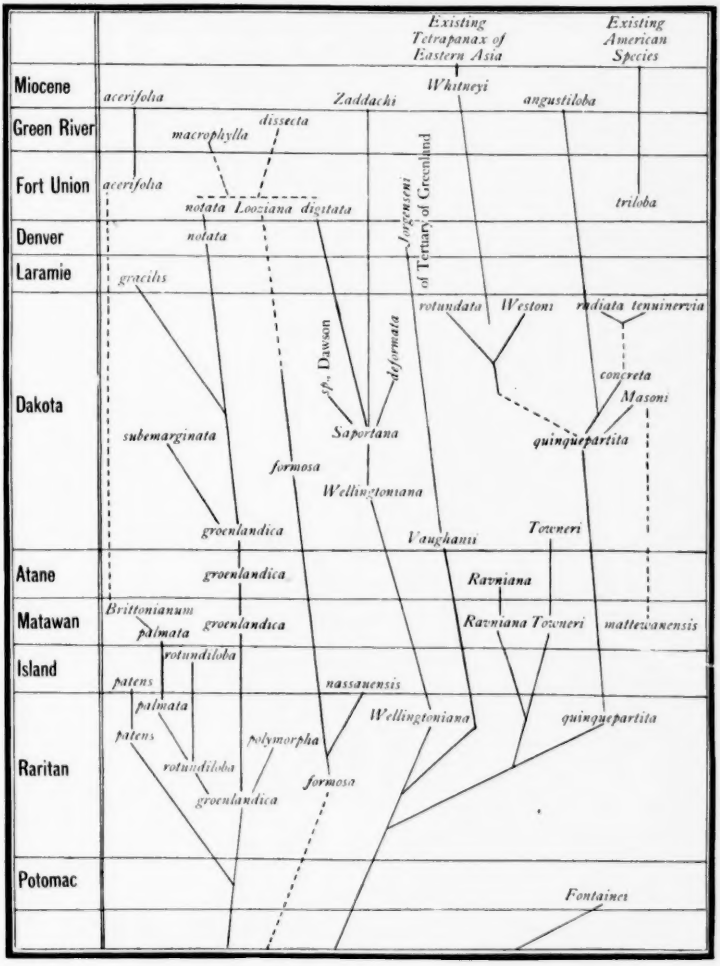
SECTION 5.

Rather small trilobate leaves with undulate or dentate margins; decurrent base; primaries three, stout, unbranched, sub-basal or supra-basilar; secondaries camptodrome and craspedodrome; lobes full, pointed. Includes leaves derived from the *Vaughanii-groenlandica* type and approaching the *notata-digitata* type of leaf very closely.

The species included are: Aralia formosa Heer, Dakota and Raritan (Europe); A. nassauensis Hollick, Island; A. Looziana Sap. & Marion, Fort Union (Europe); A. serrulata Kn., Fort Union.

SIMPLE LEAVES OR LEAFLETS.

The simple leaves referred to Aralia, following the precedent set by European paleobotanists, are four in number:


Existing Tetrapanax of Eastern Asia
Existing American Species
Miocene
Green River
Fort Union
Denver
Laramie
Dakota
Atane
Matawan
Island
Raritan
Potomac
acerifolia
Zaddachi
Whitneyi
angustiloba
macrophylla
dissecta
acerifolia
notata
Looziana
digitata
Jugensen of Tertiary of Greenland
triloba
notata
gracilis
rotundata
Westoni
radiata
tenuinervia
sp., Dawson
deformata
concreta
Masoni
subemarginata
Saportana
quinquepartita
formosa
Wellingtoniana
groenlandica
Vaughani
Towneri
groenlandica
Ravniana
Brittonianum
palmata
groenlandica
Ravniana
Towneri
mattewanensis
rotundiloba
patens
nassauensis
palmata
Wellingtoniana
quinquepartita
patens
polymorpha
rotundiloba
formosa
groenlandica
Fontaineı

Aralia Browniana Heer from the Tertiary of Greenland, which may be compared with European leaves from the Oligocene of St. Zacharie and the Miocene of Armissan.

Aralia transversinervia Sap. & Marion, described by Hollick (who notes its resemblance to Ficus) from Long Island as identical with Saporta and Marion's Gelinden leaf.

Aralia lasseniana Lx., from the Eocene (?) and Miocene (?) of California, which may be compared with leaves from the Sezanne flora.

Aralia coriacea Velen., identified by Hollick from Marthas Vineyard, the type from the Cenomanian of Bohemia.

SPECIES NOT INCLUDED in the foregoing sections are:

Aralia Fontainei Kn., from the Potomac, the remains of which are too poor for accurate diagnosis.

Aralia triloba Newb., which represents a ternately or pinnately parted leaf from the Fort Union group, which is evidently ancestral to the modern North American Aralias.

Aralia ? Waigattensis Heer, which represents a probably pinnate leaf of uncertain affinities from the Patoot beds of Greenland.

Aralia dissecta Lx., a large much lobed leaf from the Green River group.

Aralia Wrightii Kn., represented by incomplete remains from the Miocene of Yellowstone Park.

DOUBTFUL REMAINS include:

Aralia sp. Dawson, from the Mill Creek, which has been included with *Aralia Saportana* because Dawson thought that it might be that leaf.

Two forms of *Aralia* sp. determined by Knowlton from the Laramie of Wyoming; two by the same author from the Upper Eocene of the John Day Basin, Oregon; and one from the Miocene of Yellowstone Park.

The foregoing table shows the relationship of these leaves as I conceive them.

PASSAIC, N. J.

THE VEGETATION OF THE BAY OF FUNDY SALT AND DIKED MARSHES: AN ECOLOGICAL STUDY.

CONTRIBUTIONS TO THE ECOLOGICAL PLANT-GEOGRAPHY OF THE PROVINCE OF NEW BRUNSWICK, NO. 3.

W. F. GANONG.

(*Concluded from p. 367.*)

B. MESOPHYTIC DIVISION (MESOPHYTIA) CULTURE SECTION.

Consists of plants requiring the normal climatic and soil conditions of this region, useful to man and kept by his care in certain definite artificial groups.

II. RECLAIMED SALT MARSH FORMATION (MEADOW FORMATION, POIUM).

Consists, in adaptation to the very fine and hence poorly-aerated but evenly-moistened soil, of slender-rooted surface-following and hence herbaceous plants, in this case grasses or grass-like plants useful for forage or grain. Owing to the peculiar conditions here prevailing in the form of a newly-opened field (see page 295), no care from man directly is necessary to keep the plants in their desirable economic condition, for both seeding and resistance to undesirable immigrants take place naturally as long as he preserves the field in its best condition.

Includes, within an enclosure of dikes, the greater part of the area of the original salt marshes, from the sea to the head of tide on the rivers, and extended artificially into the lakes of the bogs and the bogs themselves (page 179). The formation includes three associations.

4. THE PHLEUM-AGROPYRUM, OR TIMOTHY-COUCH ASSOCIATION, OR PHLEUMETUM.

The characteristic, prevailing and most valued association of the perfectly reclaimed marsh, occurring everywhere on the higher parts of the marsh within the dikes where the drainage is good, and where the marsh soil has not been exhausted or has

not roads nor bald spots (*figs. 7, 8*). Distinguished by its familiar hay-meadow aspect, though with an unusual prevalence of couch and unusual density, luxuriance and purity of the grasses.

The association is composed of two dominant members of nearly equal prominence, with several secondary and many subordinate members, and frequent visitors.

PHLEUM PRATENSE L. Timothy.—The most abundant, characteristic, and valuable plant of the reclaimed marsh, and the dominant member of the Phleumetum. It is confined to well-drained and salt-free places, but takes possession wherever these conditions are found, hence on the highest and oldest marsh, along ditch ridges and to some extent on dikes, particularly those not exposed to the dash of the sea, and reaching its greatest perfection on the banks of aboideaued creeks. In the reclamation of marsh it is the last of the natural sequence of forms and apparently can maintain itself indefinitely as long as the drainage is kept up. It is killed immediately by salt water.

A familiar vegetation-form, typical of the grasses. Its root-hairs are plasmolyzed by 30 per cent. or less of salt water. Not native; introduced from Europe.

AGROPYRUM REPENS Beauv. Couch.—Second to the preceding in abundance and luxuriance on the reclaimed marsh, and in places even exceeding and replacing it. It forms here a highly valued hay, little inferior to timothy. It extends also upon the dikes and is the characteristic dike-top grass, especially on the dikes exposed to occasional wash from the sea, including the old abandoned dikes on the salt marsh. It also tends to come in upon the highest parts of the Staticetum.

Vegetation-form very like timothy, but able to stand salter, though not wetter places than the latter. Its root-hairs endure 30 per cent. pure salt water without plasmolysis. A native plant, found also in Europe; doubtless the form on these marshes is introduced with the timothy from Europe.

AGROSTIS ALBA L. Brown top. (Includes also *A. vulgaris*, not now considered distinct.)—Distinctly third in importance of the forms of the reclaimed marsh, occurring intermixed with the two dominant forms, but tending to occupy especially the margins

of the drainage furrows, and the lower ground, where, especially on poor marsh, it often replaces entirely the other two and becomes the dominant form. Along the roads and in places somewhat salt, it is much dwarfed. It is one of the first forms to come upon the reclaimed marsh, following after the members of the Salicornetum and Staticetum.

Vegetation-form and adaptations not especially studied; evidently more halophilous and hydrophilous than the preceding.

TRIFOLIUM PRATENSE L. Red clover.—Occurs as a characteristic companion with timothy, under whose shade it thrives everywhere on the best marsh. It varies greatly in quantity in different years, sometimes being extremely abundant (locally "clover-years"), and sometimes being nearly wanting, perhaps because it is killed by some winters and requires two years to reach full maturity.

Vegetation-form and adaptations not specially studied, but its power of fixing nitrogen comes here into account, and possibly some relation of a remotely symbiotic sort exists between it and the timothy. It is immediately killed by salt water.

TRIFOLIUM HYBRIDUM L., alsike, and T. REPENS L., white clover, also occur, but less abundantly. The two former are introduced from Europe, but the latter is native.

CHRYSANTHEMUM LEUCANTHEMUM L. Bulls-eye daisy.—Abundant in places and somewhat gregarious, and in other places wanting. Apparently it cannot compete with the timothy and couch on the best places but comes in where conditions are less perfect for those two forms. Not native, but from Europe.

Other secondary forms of minor importaace are:

Alopecurus pratensis L., bastard timothy or Durgin timothy. Rather abundant in places, and an injury to the hay-fields through its early ripening.

Calamagrostis Canadensis Beauv., blue-joint, occurs in occasional patches, but belongs rather with the hydrophytic associations.

Poa pratensis L. Occasional.

Lolium temulentum L.

Danthonia spicata Beauv.

Agrostis scabra Willd. [*A. hyemalis* (Walt.) B. S. P.]

Lathyrus palustris L. Rather common in spots on good marsh.

Ranunculus acris L. Buttercup. In patches on poorer marsh, not abundant.

Other plants occurring amongst the grasses as subordinate members or visitors are: *Fragaria virginica* L., strawberry; *Achillea millefolium* L., yarrow; *Leontodon autumnale* L., fall dandelion; *Brunella vulgaris* L.; *Viola* spp.; *Cerastium* spp.; *Epilobium lineare* Muhl., *Rumex Britannica* L.; *Rhinanthus Cristagalli* L.; *Euphrasia officinalis* L.; *Aster Novi-Belgii* L.; *Lactuca leucophaea* Gray; *Solidago neglecta* T. & G. Along the ditches grows *Convolvulus sepium* L., and there are many others.

The general adaptations of these forms to this habitat are sufficiently plain; they are typical mesophytic grasses, and the reclaimed marshes offer, as has already been traced, a typical habitat for them. But when we pass to details, the subject is not so clear.

The two dominant members, the timothy and couch, occur variously intermingled, at times in about equal proportions and again with one or the other more abundant, even to such a degree that one may occur without the other for long stretches. No physical cause is traceable for these differences, beyond the fact that the timothy seems to have the advantage on the very best parts of the marsh, and the couch where salt is more abundant. Wherever they occur intermingled, patches of one or the other often exist without visible physical determinants; and their appearance gives the impression of a resultant of slight disturbances of equilibrium in the struggle between two evenly-matched forms (or else an adjustment between two mutually tolerant forms), here one and there the other, through the slightest causes, obtaining the advantage. Both plants seem to attain their greatest perfection and purity upon the banks of the aboideaued creeks, where no doubt the somewhat coarser soil, together with the better drainage, affords a better aeration for the roots, thus permitting the more luxuriant growth. At these and other places a marked phenomenon is to be observed, having no doubt an important bearing upon the nature of competition, namely, wherever these forms are most luxuriant, there the secondary and occasional forms are less abundant, and the latter come in with the decreasing vegetative vigor of the dominant forms. In the wetter, salter, and poorer marsh the Agrostis appears more abundantly, thus forming the marginal member in that direction, as couch does in the other; but in addition it forms in places on

low marsh great areas, to the exclusion of the dominant members, in such places becoming itself the dominant form. One cannot, however, trace all of the transitions to physical causes, and in places it seems as if we were dealing here with another case of unstable equilibrium, the forms acting in mass against one another. The same phenomenon appears in the bulls-eye daisy, groups of which appear amongst the dominant members in an apparently very irregular way, again suggesting that it is not physical causes alone which are responsible for their distribution, but that it is either the result of a struggle between nearly equally-matched masses of forms, or else that there is a large measure of pure accident in the details of their distribution relatively to one another. But of this we can know nothing until we learn how the forms "compete" with one another.

This association shows one very characteristic feature of an association, lacking in those heretofore considered, namely, a distribution of the aerial parts of its members in horizontal strata. Forming the uppermost layer in the full blaze of the sun come the two dominant grasses. Nestling below the shade of their leaves, come the clovers and the Lathyrus, while in a third layer nearer the ground are the leaves of the violets, strawberries, and other low forms which I have not tried to list, all of which, of course, blossom in the early spring before the grasses have grown tall. Here again we are faced by the question as to the real ecological interrelationships of these various forms, whether we have to do (1) purely with a mixture of forms, some of which happen to be able to live in the interstices left in the growth of other forms, or (2) whether the smaller derive some benefit from the shade or other protection of the taller, or (3) whether there may be some advantage to all the members from the association, such as we can imagine the taller timothy derives from the smaller but nitrogen-fixing clover. On these matters we still have no knowledge.

As above stated, the marginal member of the association towards the Staticetum is the couch, and the marginal member towards the Macrospartinetum is the brown top, while that towards the Cnicetum is the bulls-eye daisy.

Considering now the relation of this to the other associations, it is very important to note that it is the natural association for its situation, and has not to be brought into its typical condition nor kept there by the cultivation so necessary on the upland hay meadows. When a piece of marsh is diked and drained, there follows, as we shall later note, a perfectly natural succession of plants, from the Staticetum to the Phleumetum, without any care or seeding, and the Phleumetum therefore represents the best adapted type of vegetation in this region to the conditions of the reclaimed marsh. And it is important to notice that the timothy, and no doubt also the couch, are not native, but introduced forms. There were in this forested region no mesophytic native plants so well adapted to this new field as the open-ground hay grasses from Europe, a point in perfect harmony with the general principles controlling the relations of introduced to native plants as set forth by Gray in his essay "On the pertinacity and predominance of weeds." As long as the drains are kept up, and until by long years of cropping the soil begins to weaken, this association holds its own against all comers of every sort. There is no tendency here for forest to come in, as on the upland, for reasons already explained (p. 291), nor can the ordinary weeds gain a footing until the timothy weakens through exhaustion of the soil or other cause, in which case, some scanty approach to forest may occur (p. 293). On these marshes, therefore, these European hay-grasses find an even more congenial and competition-free field than upon the upland meadows. When, however, the drainage becomes imperfect, the brown top rises to prominence, and that in turn gives way to the broadleaf as the water becomes more abundant. In these phenomena of replacement we see illustrated the first principle of competition, that a form can hold its own only in the vicinity of its optimum, and beyond that it goes down readily before another form whose optimum is being approached.

5. THE ROADSIDE WEED ASSOCIATION, OR CNICETUM.

In addition to the "weeds" associated naturally with the Phleumetum, there occurs a distinct association of upland weeds in certain places on the marshes. As this association is by no

means characteristic of the marsh, being but an extension of that of the upland, where its consideration belongs, and moreover as it is of very subordinate importance in the marsh vegetation it need here be considered but very briefly.

On the marshes the association occurs only in places especially freed from salt. Thus it occurs especially along the inner slopes of the dikes, above the frequent zone of Atriplex, and below the capping of couch (*fig. 15*), that position being particularly well freed of its salt by the excellent drainage and protection from the occasional salt spray dashed against the outer face of the dikes. In such places occur Scotch and Canada thistles (*Cnicus*, giving name to the association), yarrow in great abundance, docks, strawberry, chickweeds and many others of characteristic appearance. Again, on the ridges of earth made by the mud thrown up from the ditches, the association again appears, but here, for reasons already explained (p. 293), it tends to include some shrubs, spiraeas, wild roses, rarely alders, and a few others, with occasionally small birches, almost the only situation indeed, in which any trees are able to exist upon the marsh. There is another situation in which the association is particularly well developed, namely, on the railway embankment built, but never used, across the marshes of the Shepody near the head of tide. On this embankment, built entirely of the marsh mud, the weeds have possession, and form a tangle of spiraeas, thalictrum, yarrow, bindweed, goldenrods, myrica, sorrels, lysimachia, evening primroses, and even some lichens, small white birch and others, a genuine upland association despite the marsh soil. Another situation in which the association is well developed is on the sites of the occasional hay ricks and the vicinity of the barns on the marshes. In the former situation the bindweed is especially characteristic, and in the latter the chickweeds, but in both cases many others are associated with them. At first sight these situations, directly upon the surface of the marsh, would appear too salt to maintain such a vegetation, but, as already explained (p 293), the conditions there are really such as to promote the removal of salt. Here and there among the Phleumetum some

of these weeds may appear, but never in any abundance. Finally there are those places on the flat shallow marsh already mentioned (p. 293), from which the salt appears to have been largely removed, where a growth of bushes with some weeds may appear. These spots are of some interest as showing the tendency of the marsh, when freed from the hindering influence of the salt, to develop the climatic type of vegetation for this region, namely, the forest.

C. HYDROPHYTIC DIVISION.

Consists of plants of various aspect, but typically of soft texture and small to moderate size, provided with abundant air system enabling them to thrive in part or in whole in standing water. Contains here four formations.

III. THE WET-MARSH FORMATION.

Consists of plants capable of enduring much but not constant standing water at the roots, but otherwise able to meet the conditions of the meadow; hence composed mostly of grasses and similar forms.

Occupies all places with constant capillary but only occasional hydrostatic fresh water, hence occuring in bands between the high marsh, whether reclaimed or salt, and the bogs, and coming in on reclaimed marsh wherever the drainage is neglected. It occupies very extensive areas, perhaps equaling the Phleumetum in extent and readily distinguished from the latter by the brighter green color of at least a part of it.

It is composed of two associations.

6. THE SPARTINA CYNOSUROIDES, OR BROADLEAF ASSOCIATION, OR MACROSPARTINETUM.

The characteristic association of the reclaimed marshes wherever drainage is poor but standing water is usually absent, and hence occupying great areas on the lower parts of the marshes away from the rivers and sea and between the Phleumetum and the bog (*figs. 7, 8*). The bad aeration of the soil permits the change to blue clay earlier discussed (p. 288), which seems usually to underlie the association. The association is readily distinguished to the eye by the large size, grace-

ful habit and bright green color of its dominant form, the broadleaf.

The association is composed of but a single truly dominant member but with several secondary forms.

SPARTINA CYNOSUROIDES Willd. Broadleaf.—Preeminently the character-plant of the reclaimed wet marsh, great areas of which consist of it almost exclusively. It occurs also around the margins of the freshwater lakes and streams, to a slight extent upon the matured Staticetum, along the tide-water and nearly fresh ditches, on the new mud of the lakes in reclamation and in the bottoms of aboideaued streams. It is of very great economic importance as hay, second only in value to the timothy and couch.

Its vegetation-form embraces the usual grass type, but with unusually large air-passages, luxuriant and markedly mesophytic structure, and a considerable power of salt resistance in its roots. Will stand considerable tiding. Its root-hairs endure nearly 50 per cent. of salt water without plasmolysis, and very likely have a specific power of resistance to the somewhat poisonous constituents of the blue-clay.

CICUTA MACULATA L. Called locally (by one person) caraway (sic).—Very abundant in places among the broadleaf, raising its upper leaves and flowers much above that form and so abundant that when in flower it gives the marsh a whitish look from a distance. It is a poisonous plant, but leaves and stems appear not to be injurious when dry, though horses have been supposed to have been poisoned by eating the roots.

CAREX MARITIMA O. F. Mueller. Watergrass or fresh-water grass.—The characteristic form where there is standing water in isolated places on the marsh, in such places often replacing the broadleaf, though usually more or less intermingled with it. It stands salt water well in tiding.

CALAMAGROSTIS CANADENSIS Beauv. Blue joint.—Occurs in places as a secondary member in the wet marsh, often in large closed patches, but especially along the ditches and toward the bogs, and along the courses of the streams in the bogs, where it sometimes grows in long, dense, closed masses. Also in places upon the dry marsh in the Phleumetum.

SCIRPUS ATROVIRENS Muhl. Kill-cow (sometimes three-square?). In the wettest places, and sometimes abundant, replacing the watergrass.

Of minor importance in this association is *Triglochin maritima* L., which occurs scattered amongst the broadleaf and watergrass, and appears as much at home as upon the Staticetum. Also there occur, in a subordinate rôle, *Thalictrum polygamum* Muhl., in occasional patches; *Epilobium lineare* Muhl., abundant in places; *Lysimachia stricta* L. [*L. terrestris* (L.) B. S. P.], abundant; *Iris versicolor* L.; *Campanula aparinoides* Pursh; *Scutellaria galericulata* L., and many others of lesser importance.

The power of the chief members to endure their wet situations is sufficiently explained by their capacity for air-storage, and their ability to stand some salt by their power of root resistance. Of these members at least three, *Carex maritima*, the broadleaf, and the Triglochin, are more or less halophilous, and it is at first surprising to find them thriving so well in this situation. It is very likely, however, that this position is more salt than it seems, for it must receive much of the drainage from the higher marsh (to which, as we have seen, much salt is being raised from below by evaporation), and this may be the case particularly in the low places where *Carex maritima* abounds. This can only be determined by analysis of the soil water in that situation. It may be possible, too, that a capacity to endure salt does not carry with it any lessened capacity to endure its absence, an important point still to be determined.

The broadleaf is the overwhelmingly dominant member of this association, no other approaching it in importance, and it often occurs for great areas practically pure. The Cicuta, raising most of its foliage above that of the broadleaf, is far the most prominent secondary member, but its exact relations with the broadleaf, whether of competition, mutual tolerance or mutual advantage, remain to be determined. The marginal member toward the Phleumetum is the broadleaf itself, as it is toward Staticetum. In the former case it meets the Agrostis, and in the latter appears upon the matured salt marsh, and no doubt in the original unreclaimed condition of the marshes it occupied the great areas between the Staticetum and the bogs. The marginal member toward the bog is sometimes the broadleaf and some-

times the watergrass. The association as a whole goes down very readily before the bog-marsh, which is constantly tending to invade it, and which has to be constantly fought by the marsh-farmers, partly by improving the drainage and partly by the admission of the tide.

7. THE CAREX-ASPIDIUM, OR BOG-MARSH ASSOCIATION, OR ASPIDETUM.

The characteristic association of the transition from Macrospartinetum or broadleaf, to bog,[43] occupying the places with constant hydrostatic water in the soil, but with little above it, resulting in a mixture of grass-like and bog-like plants. Where the transition from broadleaf to bog is gradual this band is wide, elsewhere narrow or wanting. It is marked by four dominant forms.

SPHAGNUM RECURVUM vars. PARVIFLORUM (Sendt.) Warn., and IMBRICATUM (Hornsch.),[44] with very likely others.—The most characteristic plant of this association, and the invariable leader of its advance upon the broadleaf.

CAREX FILIFORMIS L.—A very characteristic member of the association, often abundant enough to give it the appearance of a meadow. Vegetation-form not studied.

ASPIDIUM THELYPTERIS Swartz. *Dryopteris Thelypteris* (L.) A. Gray.—Very abundant and a characteristic member of the association. Vegetation-form and ecological characters not studied, but being in so aberrant a position for a fern, it offers an inviting opportunity for the study of a proper physiological life-history.

POTENTILLA PALUSTRIS Scop. *Comarum palustre* L.—Also abundant and characteristic, but not studied ecologically.

With these occur several secondary forms, inclining usually to gregarious patches: *Eleocharis palustris* R. Br.; *Equisetum limosum* L. (*E. fluviatile* L.); *Eriophorum vaginatum* L., and other sedges; *Epilobium palustre* L.; *Phragmites communis* Trin. [*P. Phragmites* (L.) Karst.], locally called "quills"; *Vaccinium oxycoccus* L. [*Oxycoccus Oxycoccus* (L.) MacM.], and others, together with visitors from neighboring associations.

Characteristic of this region also, and also occurring to some extent on

[43] Omitted from *figs. 7, 8*, because when those were drawn I had intended to include this association in part with Macrospartinetum and in part with Caricetum, but further study of the subject makes it seem best to treat it as a distinct association.

[44] Identified for me by Dr. C. Warnstorf, of Neuruppin, Germany, the leading authority in this group.

the Macrospartinetum, are certain shrubs, *Myrica Gale* and *Salix discolor*, of which the former persists upon the floating bog.

To this as to the following associations I have given but little study, and have little of value to offer upon them. It is an aggressive association, constantly tending to move up upon the broadleaf marsh, the transition to which is of the most gradual character. Of all the associations of the marshland, this has the least definite boundaries, and indeed there is some question as to whether it deserves distinct rank.

IV. BOG FORMATION.

Consists of plants capable of existence in stagnant but pure water, showing, unless immersed, marked xerophytic characters (including reduction in size both of entire plant and of its parts) in adaptation to the lessened power of water-absorption by roots exposed to low temperatures.

The bogs occupy the entire marsh country above the heads of the tide on the rivers, and also places between rivers where drainage is obstructed, but their area has been much reduced in the marsh country by artificial processes of conversion back to marsh (*fig. 2* and p. 179). It includes three associations.

8. THE CAREX-MENYANTHES, OR FLOATING-BOG ASSOCIATION, OR CARICETUM.

By far the most extensive and characteristic bog association of the marshland, occupying the old marsh surface from near the head of tide on the marsh rivers to near the neighboring uplands (*figs. 2, 7*). The transition from the Aspidetum to the typical Caricetum is perfectly gradual, so that it is difficult to place a limit between the two associations. The marsh, as earlier fully explained (p. 173 and *fig. 4*), falls away gradually from tide-head, so that leaving behind the high marsh with its Phleumetum we reach a somewhat wet marsh with its Macrospartinetum and a constantly wet marsh with its Aspidetum, and finally come to a marsh with constant standing water above the surface, and here begins the Caricetum. The characteristic dominant plants are sedges of several species whose copious interlacing air-storing rootstocks form a mat, which floats upon the surface of the water as it deepens (*fig. 4*), and which becomes three or four feet in

thickness. It floats upon a foot or two of water, beneath which is the true marsh mud, blue for a few inches from the surface, and below that red to the bottom. As a rule the bog is firm enough to walk upon, though it trembles beneath the tread, but in places it is unsafe.

The dominant plants are, of course, the sedges, chief of which are the following:

Carex filiformis L., and *Eriophorum vaginatum* L., from the preceding association, are equally or nearly as characteristic of this; also *Carex stricta decora* Bailey, *Carex Magellanica* Lam., *Eriophorum gracile* Koch, and others.

With these are associated as a principal though hardly as a dominant member *Menyanthes trifoliata* L., the Buck-bean, which is especially abundant on the margins of streams and ponds, and with it is *Calla palustris* L. Among the sedges occurs some Sphagnum, but this, in the floating bogs, is by no means a dominant plant.

Upon this floating mat grow many other plants, many of them distributed in groups the determinants of which are not plain. Thus, especially near the transition occur large areas of very abundant *Equisetum limosum* L.; in other places *Eleocharis palustris* R.Br., is densely abundant. Further out large areas are nearly covered with *Typha latifolia* L. (cattails); again groups of *Phragmites communis* Trin. (quills) occur. *Myrica gale* L. is also abundant. Among less abundant plants are *Juncus Canadensis* J. Gay, and *J. Balticus litoralis* Engelm., *Sparganium simplex* Huds., *Sarracenia purpurea* L., *Drosera rotundifolia* L., *Epilobium linearis* Walt., and a few others. But I have not attempted to make a proper ecological study of these bogs, which I hope upon another occasion to consider much more fully.

9. THE HEATH, OR FLAT (SOLID) BOG ASSOCIATION, OR ERICETUM.

I have not attempted to make any ecological study of this association. It occurs mostly around the margin of the Caricetum on the parts furthest from the sea, and between the rivers, as at Sunken Island (*fig. 7*), and is readily distinguished by the presence of abundant trees of larch and black spruce, and

the abundant heath bushes.[45] In places on the floating bog, especially near its margin, one sees occasionally dense mats of Hypnum several feet across, indicating no doubt the beginning of flat bog formation. In general this association occurs at the oldest part of the bogs and hence probably represents the conditions towards which the floating bog is tending. It tends to occur also in strips along the contact of mainland and the Macrospartinetum, where it begins to merge into swamp, as later to be noticed.

10. THE SPHAGNUM, OR RAISED BOG ASSOCIATION, OR SPHAGNETUM.

In a few places only, near the margin of the Caricetum, occur small areas approximating to the true raised type of bog, consisting almost entirely of Sphagnum rising above the general water level of the basin, with dwarfed heath bushes but no trees, and generally showing the characters of *Hochmoor* which I have already described in the first work of this series. Small areas of this character also occur in the Sunken Island. But I have not tried to work out their relations to other types of bog, and the subject remains for future study.

V. WATER MARGIN FORMATION (NEMATIUM).

The marsh and bog rivers above the influence of the tide everywhere exhibit a dense marginal vegetation (Typha, Sparganium, Acorus, Lysimachia, Chelone, Dulichium, etc.) differing in different parts of marsh or bog, and divisible into three or four associations. I have not, however, made any attempt to study these in detail. Another association exists on the margins of the lakes, and yet another in the bottoms of the aboideaued streams. There is also of course a plankton formation in these streams, but I have not studied it.

VI. THE SWAMP FORMATION (HELORGADIUM).

In most places, at the contact of reclaimed marsh and upland, occurs a region of poor drainage in the form of a narrow strip. On the wet marsh, along with the Macrospartinetum, this strip is

[45] Not all trees on the bog, however, indicate the flat bog, for many of them, as shown by soundings made by engineers of the Misseguash Marsh Co., are growing upon islands slightly submerged by the bog.

usually occupied by flat bog (Ericetum), but on the dry marsh it is more likely to form a strip of swamp, with alders, black spruce, and blue flag. This forms at least one association, probably more, but I have not attempted to study it, and it remains for future investigation.

The succession of the plants of the marshland in space and in time.

The succession of the plants of the marshland within associations, both in space and in time, and of the associations within the formations, have been described in the preceding pages, but we may here summarize the subject and attempt to represent it graphically. Then we must consider the natural succession which takes place in the reclamation of the marshes.

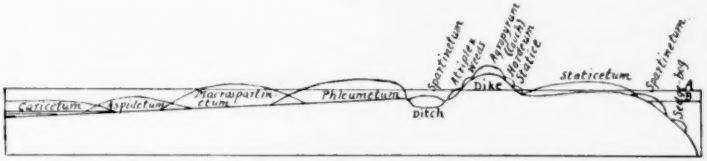


FIG. 15.—Diagram to show the distribution of the principal associations of the marsh land in relation to one another. The tops of the curves show the places of maximum development of the association, and the places where they overlap are the places of competition. *A* is extreme high tide level, and *B* ordinary high tide. The "ditch" is not a drainage ditch but one of those from which mud has been taken for the dikes.

The succession of the associations on the marshland is about as represented in *fig. 15*. The form given to each association is intended to represent its culmination at its optimum of size and vigor, and to show that the associations only mingle on their margins when their optima are past. These relations may be brought out in another manner and correlated with the distribution of the prepotent physical factors of water and salt, by means of the curves of *fig. 16*, which, however, it is to be remembered, are not constructed from actual measurements, but only ideally from observation. They have their chief interest as a prediction of the way in which such facts will ultimately be represented.

The distribution of the associations on the dikes is notable,

and needs some comments (*fig. 15*). The physical conditions upon the dikes are plain. The situation is a particularly well-drained one, but on the outer face of those exposed to the sea there must be more salt than upon the inner faces, due to the occasional wash of the sea at high tides during storms. At all events especially on the more exposed dikes, the outer slopes usually show a more halophytic facies than the inner. On both faces there is a distinct zonation, which differs somewhat in different places, but appears most characteristically, especially on dikes exposed directly to the sea or lower courses of the tidal rivers,

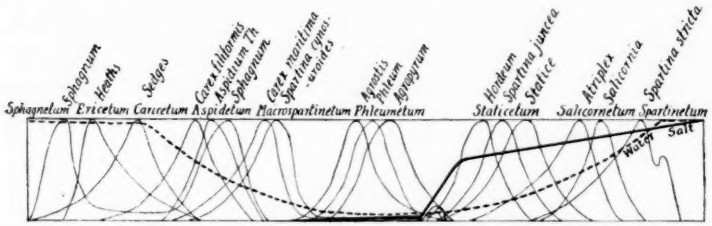


FIG. 16.—Diagram to show the distribution of the principal associations and of their prominent species in relation to the amounts of water and salt. The species curves show the approximate range of the forms within one another's habitat. The two members of the Macrospartinetum can endure some salt; hence their extension as here represented. The second summit of the Spartinetum represents the "sedge-bog."

to be as follows: On the outer face, the lowest zone, occupying the angle, is usually the Statice, but is sometimes Puccinellia; above this is a zone of Hordeum and above this the couch, the almost invariable dike grass, here evidently fully at home. Occasionally Atriplex occurs between Hordeum and couch. Now the Statice is the usual marginal member of the Staticetum, while the Hordeum comes in early upon that formation when maturing and the couch comes upon it later. There is plainly then upon the outer face of the dikes a general repetition of the order in the association, though the *Spartina juncea* is not, as far as I have noticed, in its place between Statice and Hordeum. The zonal arrangement, however, often shows Atriplex in place of the Statice, and the Hordeum may be wanting. On the inner face of the dikes, there is usually a band of Atriplex at the lower angle, especially when, as is usually the case, there is a row of

ditches containing stagnant and hence saltish water, just within the dikes, occupied by *Spartina stricta*. Above this Atriplex comes often, if not usually, a band of common roadside weeds, a part of the Cnicetum, while above it is the band and cap of almost invariable couch. This arrangement is sometimes different, and I have even seen a case where the top of the dike was occupied entirely by Atriplex, with a band of couch on each face of the dike below it, and other variants occur, the whole being much influenced by the position and age of the dike.

We pass now to consider another important phase of this subject, namely the natural succession of the plants on new marsh which is being reclaimed from the sea. It is rarely nowadays that a new piece of marsh is diked and reclaimed from the beginning, but what is practically the same thing occurs in numerous places, where the marsh is being renewed by the tide. When a piece or body of marsh shows a lessening of fertility, either through the growth of bog or other causes, the dikes are broken down and the tide admitted. The higher tides usually flow readily over it (an evidence, as I believe, of the gradual subsidence of the region), kill most or all of the vegetation upon it, and begin to deposit new mud. This is allowed to continue until several inches of mud have been laid down, a process requiring usually two or three years; then the dikes are re-built, the drains are opened, and the marsh is left to itself. A vegetation at once springs up upon it, which goes through a series of changes, ending in the development in four or five years of the Phleumetum or best timothy grass, and without any aid from man beyond keeping the drains in order. This succession can be followed in various places and is about as follows: When the tide first flows upon the marsh ,the plants show very diverse degrees of resistance to it. The bog plants, the various woody bushes, the clovers and the timothy are killed at once, it is said by a single tide. They turn white or brown and dry up, the bushes turning almost black, as if scorched by fire. On the other hand the watergrass, the broadleaf, the browntop, show a considerable degree of resistance, while the couch can stand

for some time on the higher tussocks.[46] I have not determined the exact cause of the death of these forms, but presumably it is due to the plasmolysis of the root hairs, and consequent loss of ability to absorb water, followed by a drying up. To this, of course, may be added some positively poisonous action of salt upon the protoplasm. The tide deposits layers of the rich mud, and upon this, while undiked, there tends to spring up a large development of the Salicornetum. In particular, there appears during the process of tiding an open growth of Suaeda, Salicornia, and Atriplex, all of which grow large and luxuriant. Of these the Suaeda appears to become most abundant, and is a large, diffuse, straggling plant quite superior to its small form on the river banks. The Salicornia also grows very luxuriantly, spreading diffusely in this situation. With these plants comes in some sedge, though I have not noticed that it becomes very abundant or luxuriant. Such appears to be the natural condition of marsh in reclamation. When the dikes are restored the first phenomenon observable is the large increase in size and abundance of these forms. They fill up the ground, and the Atriplex in particular grows even waist high. The remarkable luxuriance of the members of the Salicornetum under these conditions shows how far they are, upon the marshes, from occupying their optimum situation, from which they must be kept by the dominance of the other associations, a subject of much importance in connection with the nature of competition. But along with the increase in size, other forms immediately begin to come in, especially some members of the Staticetum, the *Spartina juncea*, Triglochin, and especially the Puccinellia, and the Hordeum, which is ubiquitous in such positions. Closely after these, however, comes the couch, and right after it the Agrostis. Such is the condition at the end of the first year, after which the timothy follows; and in the fourth year it becomes abundant. As the new forms come in the older tend to die out, so that finally, after a succession of forms answering to the natural succession in space on the marsh, the timothy takes natural

[46] This resistance is taken advantage of by some farmers, who admit the tide sparingly and are able to obtain some renewal without totally losing an annual crop. But it is not considered a profitable method.

possession, all the others except the couch disappearing. This, however, is the summit of the series; nowhere, excepting on the ridges along the ditches and in a few exhausted spots, where a low shrub vegetation appears, is anything higher developed. The timothy stands out as the best adapted plant in all this country to the conditions prevailing on the reclaimed marsh. In this process of reclamation, there is a grand opportunity to study the nature of competition, the problems of which, however, cannot be settled by observation alone, but must be attacked by experiment.

The above appears to be the normal succession upon places where high marsh is built; in the low places the succession is somewhat different, leading through watergrass ultimately to broadleaf, which by improvement in drainage may lead to couch and timothy. It is said by the farmers that the succession of plants depends much upon the way the drainage is managed.

There is another place in which the succession may be followed, namely in the lakes in process of reclamation, and I have seen it particularly well illustrated in Germantown Lake in Albert county, to which the tide is admitted by a canal. The tide has built into the lake long low points of marsh mud, which are at once taken possession of by a rank growth of *Spartina stricta* (sedge) immediately above which, on the higher parts, comes a dense growth of broadleaf. Right after the latter come scattered tufts of dense browntop, which is fairly abundant, and after this comes the couch. Here too is afforded a very favorable opportunity to study competition, which, however, I had not the time or means to utilize.

Conclusion.

The observant reader will not need to be told that the present study is highly defective and inconclusive, to a degree which no one can realize more than does its author. Yet this very defectiveness emphasizes an important lesson, for, while it is in part the fault of the author, it is not wholly so, but is in a large measure made necessary by the present imperfect state of our

ecological knowledge and methods. The study does make fairly clear, however, the directions in which research must now proceed, and upon this I desire to offer some comments.

The idea of ecological plant geography, the broadest and most important phase of ecology, is to interpret the physiognomy of vegetation; to tell precisely why each plant is where it is, in the company it is, and of the form, size, color, texture, etc. it is. Each plant, as it stands in nature, is an adjustment or equilibrium between its physiological powers and properties on the one hand, and the properties of the environment, physical and biological, on the other. Now, for a full understanding of these matters four principal things are needful.

First, a collection and description of the actual facts as to the kinds of plants which occur in a given region, as to their visible features, and as to the way in which they are grouped. Our present-day ecology, especially that which is being actively pursued in this country, is strong in this descriptive work, to which indeed it is well-nigh confined, and it is giving an excellent basis for future advance. In the present paper I think these facts about the marshland vegetation are fairly represented. Even from this point of view the study is defective in one respect, common to most of our ecological studies, namely, the descriptions apply to the summer only; if followed through the year (as it should, but for practical reasons could not, be), it might, and probably would, lead to conclusions somewhat different in details, as well as to much additional knowledge.

Second, an exact study and clear expression of the facts as to the physical features of the environment which can affect plant life. For the study of the physics of the atmosphere, the methods have been thoroughly organized by meteorologists, but we need some way of expressing meteorological results in a form for ecological use. It is very common in ecological papers, as in the present one, to give elaborate tables of temperature, precipitation, etc., and then to dismiss them with a few words of general comment. This shows either that meteorological data are obtainable more copiously and exactly than needful for ecological use, or else, as is more likely, they are not expressed in a

form in which we can make ecological use of them. Some advance has been made in this direction by such curves as Drude uses in his *Hercynische Florenbezirk* (p. 71), but these need further development. In the study of the physics of the soil, however, the ecological importance of which is becoming constantly more manifest, it is very obvious that, despite the rapid advances now being made, the methods of investigating and of representing the facts are still far from developed and wholly insufficient for ecological uses. The extension of knowledge in this direction is, I believe, the greatest desideratum of ecology for the near future. In thus emphasizing the deficiencies of our knowledge of the physics of the plant's environment from the ecological point of view, I would not underrate the positive knowledge we have, which is considerable. But it is notable that this knowledge is of a very general sort and not expressible in definite ecological form, as shown by the general and even hazy way in which it is commonly stated in current ecological literature, including the present paper. In fact, vague generalization and nimble guessing (much of it, no doubt, good guessing, but still guessing) are more characteristic of the physical part of our current ecological literature than is precise statement; and the expressions "probably," "doubtless," "in a general way," form a considerable part of present ecological language. All this is evidence that in our ecological discussions we have reached about the limit of possible advance with our present knowledge of the physics of the environment and of how to use the knowledge we have. Indeed, this point was reached some time ago, and much of recent ecological literature has been so barren of real advance as to bring upon ecology a reproach which it must be admitted it largely deserves. This is the more unfortunate since even the methods of ecological description have not substantially improved. I can say this with the greater frankness since my own study herewith presented so obviously reflects the prevailing formalism and deficiencies in this respect, though I have made some attempt to improve at least the method of description of the vegetation. There can be no question, I believe, that further substantial eco-

logical advance is not possible until we make a direct attack from the ecological standpoint upon the subject of the investigation and representation of the facts of the environment, especially of the soil. Now this obviously cannot be done, as most ecological work is now being done, by busy teachers who can devote to field work only a few weeks of their summer vacations. It can only be accomplished by the systematic work of trained investigators, who, with a fully and properly equipped laboratory established in the field at the place to be investigated, and with ample assistance to aid in the mechanical work, can devote their entire time to the subject for months or years until the problems are solved for that region. The laboratory must obviously be in the field, since the conditions vary so much in the different seasons and under the various local conditions. Thus, and thus only, I believe, can we make any further real advance in ecological plant-geography.

Third, there must be made a thorough study not only of the structure and development of the important plants which give character to the different parts of a vegetation, but also of their physiological characteristics quantitatively expressed. Thus, we need to know for each kind of dominant plant its transpiration power, and the extent of its possible regulation under various circumstances; its water-absorbing power; its capacity for air storage; its power and limits of resistance to salt or other unfavorable substances and influences; its cardinal temperature-points for growth and for its other physiological properties. For this study it is indispensable that methods and apparatus be developed by which the various facts may be ascertained with ease and precision, and the results expressed or represented in a form to make them available for ecological use, that is, so that they may be compared and correlated with the physical data. Very important in this connection is the determination of the physiological plasticity of the plant, and in how far adaptation to a new influence weakens or destroys adaptation to an older. Hitherto, in our studies of adaptation we have laid great stress upon the study of structures in relation to adaptation to environment, and much knowledge of this subject has been accumu-

lated, while physiological adaptation, the study of the accommodation of the protoplasm itself to outside influences, has received little attention. Yet this is the most important subject of all in adaptation; for structure, so far from representing the important feature in the adaptation of the plant to its environment, is simply an external manifestation of the way in which the protoplasm brings itself into better touch with the environment. It is an expression of a degree of physiological properties, and it is the properties and powers of the protoplasm itself which is the important thing. All such data are essential to the full understanding of the real nature of the vegetation-forms, those units of the ecologist; and in this direction, viz., the determination of physiological life histories of important plants, there lies not only an indispensable approach to future advance in ecology, but a most attractive field of research for its own sake. Such studies, and such only, will enable us to understand the true natural history of individual plants, and will help to bring the day when our "manuals," in addition to giving us the details upon which the classification of our plants is based, will give us also such information about their lives and habits as will enable us to understand their places in nature. These studies may in part be followed in university laboratories, but for the most part they can be carried on only in field laboratories, such as have already been mentioned as needful for the study of physical problems, and here both classes of problems, similar in general methods and inseparable in results, can best be investigated together.

Fourth, a knowledge of the true nature of plant competition and cooperation is essential. The fullest knowledge of the physical environment, and of the power of the plant to respond to it, would only enable us to explain the general situation and vegetation-form of plants in cases where each individual was free from any interference from others. But in fact, as we know, plants are rarely or never so situated, for, massing together, they profoundly affect one another's distribution and form. The study of vegetation, therefore, of masses of plants, involves this important element of their effects upon one

another. Or we may express the situation thus. Ecological plant geography is the study of the actual adaptations of masses of plants as they grow together in nature. The physics of the environment, plus the physiological properties of the plant, tend to give as a resultant a certain general vegetation-form; this, plus cooperation and competition, gives the actual groupings in a vegetation.

That plants do in some way compete with one another, that upon the same ground some kinds can drive others out and take possession, is, of course, evident to observation. That, on the other hand, certain kinds of plants can combine and cooperate for the common good is, I think, equally true. In both cases we know some of the general causes which determine the results of both competition and cooperation, but as to the details we know nothing. Seven years ago Warming, in his great book, said: "There is scarcely a more attractive biological field than to determine what the weapons are with which plants force one another from their positions," but today we know no more of that subject than when Warming wrote those words. Yet ecological plant geography cannot advance, nor can we understand the vegetation of a country or district, until we understand this subject, and we but blind ourselves and only imperfectly convince others by our present generalizations. The crucial point in competition is this: by what weapons or methods does one plant overcome another, when the result is determined between the plants and not by the environment. In a broad way we can often see general reasons why one plant should dominate another; the more rapid growth of one kind, or larger size, or the replacement of a shade-loving by a sun-loving kind, or the entrance of a new kind when one form has exhausted the needed minerals from a soil, etc., seem to give an ample explanation. But even in these cases, and especially in the many cases where the kinds seem evenly matched, we do not know precisely the method by which one kind manages to displace another. It is obviously by means of no visible carnal weapons such as animals use, nor is it a mechanical forcing aside of a weaker kind, for often there is ample standing room for the vanquished with the victor.

Some of the phenomena of competition seem to imply that each plant is able to control by some chemical or other method still unknown, a certain sphere of influence about it, a limited area of space of which it is the center and from which it can exclude others, and that this sphere of influence, like other adaptive features of the plant, is modifiable adaptively. Gregarious forms would be such as grow together so closely that these spheres touch, excluding other forms, and before the advance of such a phalanx other forms of lesser vigor must all go down. Elsewhere these spheres, rigidly maintained against an enemy, might be relaxed to admit a friendly or cooperating form, and other of the phenomena commented upon in the preceding pages, might find an illuminating explanation in such a conception. But it is all pure speculation, and can be settled only by careful field experiment. Until this is given we shall not know whether associations are mere mixtures, or are to some extent cooperative communities, and if the latter, what the nature is of the bonds which unite their members. I have no question that in a properly equipped field laboratory, such as has already been mentioned, competent investigators, working with an experimental piece of ground, could solve this most vital of questions. Fortunate will he be who first has the proper opportunity to attack it!

NORTHAMPTON, MASS.

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NOTES ON GARRYA WITH DESCRIPTIONS OF NEW SPECIES AND KEY.

ALICE EASTWOOD.

ANYONE who has done field work in California among the brush-covered hills will appreciate the puzzling character of Garrya. Like Salix, it is dioecious and is rarely found in flower and fruit at the same time, so that in the different herbaria of the country the species are quite inadequately represented and the types very unsatisfactory.

It is impossible with the present knowledge of the genus to attempt more than a provisional arrangement. The species bloom in the depth of the winter months, when few think of collecting plants; they fruit in August or September, when it is dangerous in many places to explore the dry hills on account of the scarcity of water and the density of the brush. In some years the fertile bushes bear no fruit and always seem few in comparison with the sterile ones, so that it is possible to pass through a region where these shrubs grow, at the right time of the year, without discovering a single plant in fruit.

For some time I have been interested in the two species that grow on Mount Tamalpais, across the Golden Gate from San Francisco. They seem to represent the two groups into which the Californian species fall. *Garrya elliptica* has peculiar pubescence, consisting of curly hairs which form a more or less dense tomentum on the lower surface of the leaves and young fruit. The berries, when ripe, are not unpalatable. The seeds are surrounded with an acid pulp which is very slightly tinged with bitterness. *Garrya rigida*, the other species, has fruit so bitter that one taste will suffice for a lifetime. This is commonly known as "quinine-bush." The pubescence is sparse and consists of almost straight, silky hairs, regularly appressed upward.

The genus may be divided into two great sections, the northern and the southern, the former characterized by non-branching aments; the latter with some or all of the aments branched,

generally near the base. There are also two kinds of pubescence in each class. In one the pubescence on the lower surface of the leaves is formed of curly or curly and wavy hairs intermixed to form a dense tomentum; in the other the pubescence, when present, consists of almost straight hairs, generally upwardly appressed and silky in texture.

In the following key these characteristics have been used to classify the different species, and, until they are better known in flower and fruit, it seems the only possible way and may perhaps accord with the natural affinities.

PROVISIONAL SYNOPSIS OF THE SPECIES OF GARRYA.

* *Aments not branched.*

Pubescence of tangled, curly, or wavy hairs.

Garrya Veatchii Kellogg Proc. Cal. Acad. **5**: 40.
Palmeri nom. nov.
undulata var. nov.
elliptica Lindl. Bot. Reg. *pl. 1686.*
Congdoni sp. nov.

Pubescence of upwardly appressed, almost straight, silky hairs.

Garrya buxifolia Gray. Proc. Am. Acad. **7**: 349.
flavescens Watson Am. Nat. **7**: 301.
pallida Eastwood Proc. Cal. Acad. III. **2**: 267.
rigida sp. nov.
Fremontii Torr. Pac. Rail. Rep. **4**: 136.
laxa var. nov.

* * *Some of the aments branched.*

Pubescence of curly hairs.

Garrya ovata Benth. Pl. Hartw. 14.
Lindheimeri Torr. Pac. Rail. Rep. **4**: 136.
macrophylla Benth. Pl. Hartw. 50.
oblonga Benth. Pl. Hartw. 50.
longifolia Rose (in herb).[1]

[1] This is doubtfully placed here. There seem to be two different species of Pringle's collection with this name, and I do not know which is the type. One seems too near *G. laurifolia.*

Pubescence of upwardly appressed, silky hairs.

Garrya laurifolia Benth. Pl. Hartw. 14.
salicifolia sp. nov.
Wrightii Torr. Pac. Rail. Rep. **4**: 136.
Fadyeni Hook. Ic. Pl. *pl. 333*.

GARRYA VEATCHII Kellogg.—Leaves ovate-lanceolate, acuminate at apex, rounded or oblique at base, entire or the youngest leaves very slightly undulate; upper surface except in youngest leaves smooth and shining, lower densely clothed with white tomentum consisting of short, very fine, closely curled hairs. Berries densely clustered and rounded at base without a sign of point or pedicel, apex beaked by the united base of the styles, calyx divisions minute, completely hidden amid dense hairs at top, a short distance below the styles.

The berries are so closely clustered and sessile that none of the involucres except the very lowest are visible in the type. The type was collected on Cedros Island by *Dr. Veatch* and is now in the Herbarium of the California Academy of Sciences.

GARRYA VEATCHII **Palmeri,** nom. nov. (*G. flavescens Palmeri* Watson Bot. Cal. **1**: 276).—Placed here on account of the character of the pubescence, which is that of *G. Veatchii* instead of *G. flavescens*. Distinguished from typical *G. Veatchii* by the broader leaves, generally oval, shortly acuminate or almost aristate, slightly undulate. Berries cuneate at base, the lower almost pedicellate; apex beaked by the united base of the styles and the two calyx divisions, which are prominent and close to the base of the styles; involucres even of the ultimate flowers easily distinguished and the lower conspicuously foliaceous.

The type was collected by *Dr. E. Palmer* at Milquatay, 60 miles (95 km) from San Diego on the road to Fort Yuma. This, as well as two specimens collected by *C. R. Orcutt*, one near Campo, Lower California (no. 900) and one from Hansons, Lower California, April 21, 1885, are in the Gray Herbarium. Here belong also no. 899 (*H. M. Hall*) collected on dry slopes in Lytle Creek Cañon, Southern California, April 24, 1898, and no. 2805 (*L. R. Abrams*) from the same locality, July 15, 1902.

GARRYA VEATCHII **undulata,** var. nov.—Differs from typical *G. Veatchii* in having oval or elliptical obtuse or aristate leaves

with undulate margins; berries cuneate at base and so densely clustered as to conceal upper involucres; calyx divisions hidden in dense wool and at some distance below the base of the styles.

This is represented in the Gray Herbarium by specimens collected by *O. D. Allen* at Pasadena, February 1885, and by a fragmentary specimen collected by *H. C. Ford* at Santa Barbara, April 1881. The best and most complete specimens have been collected by *George Grant* on Echo Mountain, back of the hotel. This mountain is a spur of Mount Lowe.

GARRYA ELLIPTICA Lindl.—This species is common in the Coast Mountains and extends from the Columbia River on the north to the southern part of the Santa Lucia Mountains on the south. Easily distinguished from other species by the large oval or elliptical leaves, strongly undulate. There is a great contrast between the almost smooth, dark green, glossy upper surface of the leaves and the white tomentose lower surface clothed with densely matted curly and wavy hairs. The calyx divisions are so small, so close to the pointed base of the styles, and so concealed by the dense wool that it is only by the most careful search that they can be found. The berry is abruptly short-acuminate at base. The bushes that grow in the inner range of hills have narrower and more pointed leaves than those that grow near the coast; but in all other respects seem identical.

Garrya Congdoni, sp. nov.—Stems brownish-red, youngest twigs white-tomentose. Leaves narrowly oblong to oval and elliptical, 3–5 ^{cm} long, 1–3 ^{cm} wide, tapering at both ends with recurved mucro at apex; petiole stout, keeled, 5 ^{mm} long; margins glabrous, thickened, entire or slightly undulate; upper surface glossy, yellowish-green, sparingly pubescent with curly or wavy hairs, the lower clothed with dense white tomentum consisting of curly and wavy hairs somewhat upwardly appressed but matted and tangled; veins distinct. Staminate aments numerous, varying in length; involucres cuneate at base, short-acuminate at each end with an obscure rounded tooth on each side of the middle, densely tomentose throughout, pedicels surpassed by the perianth; perianth with oval divisions united at top and clothed with long, wavy hairs.

Neither the pistillate flowers nor the fruits have been collected. The type was collected by *J. W. Congdon*, in whose honor it is named, near

Coulterville, Mariposa county, January 1898. Besides this, which was distributed by Mr. Congdon to various herbaria there is another specimen in the Gray Herbarium, collected by *Mr. Congdon* at Benton Mills, Mariposa county, July 5, 1898; also one in the Herbarium of the California Academy of Science collected by *Dr. C. Hart Merriam* on the Merced River, September 1902. A specimen collected by the author on the ridge between New Idria and Hernandez in San Benito county with immature fruit is also placed here. The young berries are rounded or abruptly pointed at base; the two calyx appendages are minute, closely appressed to the styles, and so densely clothed with long wavy hairs as to be hidden by the dense pubescence of the pointed base of the styles.

GARRYA BUXIFOLIA Gray.—Low, spreading shrub; leaves in typical specimens small, about 2^{cm} long, 1–1.5^{cm} wide, oval to elliptical or ovate, entire mucronate rounded or slightly oblique at base, the upper surface dark glossy green, lower densely white tomentose with almost straight silky upwardly appressed hairs; berries becoming subglabrous, beaked base of styles with small calyx divisions appressed.

The type was collected on Red Mountain, northern Mendocino county. Howell's specimens from Waldo, Oregon, have much larger leaves and smaller calyx divisions. It is abundant on the hills along the Crescent City road near Gasquet's.

GARRYA FLAVESCENS Watson.—Shrub with yellowish-gray aspect, young stems tomentose with a close, upwardly appressed pubescence of fine, almost straight, silky hairs; lower surface of leaves with similar pubescence, upper with scattered hairs irregularly appressed, Leaves broadly oval to narrowly elliptical, pointed at both ends, apex tipped with a sharp recurved mucro, veins strong and distinct; petioles 0.5–1^{cm} long; margin glabrous, entire.

The type specimen from the Gray Herbarium, collected by *Dr. E. Palmer* at St. George, southern Utah in 1887 (no. 183½), has unusually long and slender styles on the very immature fruit. A specimen from Kanab Plateau, collected by *Alfred Weatherill*, August 5, 1897, has fruit more mature, with the styles almost gone. On none of the berries examined could any trace of calyx divisions be found. This species seems to be confined to Utah and New Mexico and the adjacent country probably, but it is very near the next.

GARRYA PALLIDA Eastwood.—Distinguished readily in the field by the glaucous-gray tone of the entire plant, which does

not come from the pubescence but is noticeable where the leaves are almost smooth. Leaves large, oval to elliptical, entire, acute at each end with a recurved mucro at apex; petioles 1–1.5 cm long; pubescence sparse, upper surface of leaves generally glabrous except when young. Involucres deeper than in *G. flavescens*, being about 3 mm at the middle while the preceding is about 1 mm. Calyx divisions close to the beak of the base of the styles and concealed in the young fruit by dense hairs.

Grows in the Southern Sierra Nevada where *Pinus monophylla* is found or in the Coast Mountains where *Pseudotsuga macrocarpa* grows. Specimens are in the Herbarium of the California Academy from Kings River Cañon, San Emidio Cañon, Tehachapi, Kaweah Cañon, and Zaca Mountain, Santa Barbara county. The last-named specimens were collected by the author, June 1902, and have smaller, narrower leaves than specimens from other localities.

Garrya rigida, n. sp.—Erect shrub, 1–2 m high, with older stems gray-brown, becoming darker with age, youngest generally red though sometimes green, glabrous throughout except for a sparse, appressed pubescence on the younger stems, leaves, and bracts. Leaves elliptical-obovate, thick, coriaceous, entire, bright green, noticeably reticulate, 5 cm long, 2.5 cm wide on an average, tipped with an obtuse mucro, tapering at base to a thick petiole 1 cm long; petioles connate-clasping. Aments fascicled or sometimes solitary at the ends of the branchlets, 1–1.5 cm long or less, with 5–15 involucres connected by the peduncle which between each involucre becomes longer than the stamens; lowest involucres with recurved foliaceous tips as long as the body of the involucre, upper tipped with stiff points which diminish towards the ultimate flowers; body of the involucre green or red, generally tipped with green, pubescent at the middle and base. Flowers on filiform pedicels, 5–6 mm; divisions of perianth green, 1-nerved, linear, white-hairy at top, 5 mm long, glabrous on inner side, united at tip, but later separating; stamens green, changing to yellow, with anthers 2 mm long, longer than the filaments. Pistillate aments rigid, 1–4 cm long, with the involucres closely imbricated and green, in other respects resembling those of the staminate flowers; flowers apetalous, 6 to each involucre, 2 styles to each pistil, black, narrowly subulate, sparingly clothed with

white hairs, as long as the ovary; ovary green, clothed sparingly at base and densely at apex with white upwardly appressed hairs. Fruit slightly pubescent, purplish-gray, densely clustered, very bitter.

Grows in the Coast Mountains of California and its range seems to be from Trinity to Monterey counties. The type locality is on Mount Tamalpais. It is quite abundant on what is known as the Bill Williams Trail from Eldredge Grade to Rock Spring, and has also been found along the railroad track.

This species has been included under *Garrya Fremontii* Torr., which is a species of the Sierra Nevada and the mountains of northern California and Oregon. The southern limit of *G. Fremontii* seems to be the Yosemite, where it is abundant along the road from Inspiration Point and also near Vernal and Nevada Falls.

Garrya rigida is different from *G. Fremontii* in habit, pubescence, inflorescence, and the fruits. Those of *G. rigida* are purplish, tinged with gray; those of *G. Fremontii* are black when dry.

It is much nearer *G. pallida* Eastwood, but differs in the bright instead of glaucous green foliage. Flowering specimens of *G. pallida* have not been collected, so good comparisons cannot be made; but the appearance of the two as they grow is quite different, as well as their range and environment.

GARRYA FREMONTII Torr.—Typically almost entirely glabrous, leaves rather small, not more than 4^{cm} long, and 2^{cm} wide, with cuneate base and mucronate apex. Staminate aments slender, with a few scattered hairs, more dense on the margins and near the tip of the two teeth. The stamens seem to be yellow and are exserted from the open sides of the sepals, which are united at the top. As the type has only staminate flowers it is impossible to compare the other parts with what seem the same species from other parts of the state.

The nearest of all the specimens in the Herbarium of the California Academy of Sciences is one collected by *C. A. Purpus* on Eel River, Mendocino county. This has much larger leaves but the staminate catkins are the same. Specimens from the Yosemite with immature fruit have the large leaves of the Eel River plants and almost sessile berries with inconspicuous calyx divisions. These characteristics hold true also with specimens collected on Mount Bohemia, Oregon, in the Callipoia Range, June 14, 1902, by *P. E. F. Peredes.*

GARRYA FREMONTII **laxa**, var. nov.— Distinguished from the forms included under *G. Fremontii* by the longer petioles of

the leaves, 2^{cm} or more, the more loosely fruiting aments, the peduncles more than twice as long as the involucres, and the pedicels equaling or surpassing the involucres. The berries, which turn black when dry, are tipped with the two styles and the conspicuously spreading calyx divisions opposite, giving the appearance of four styles when the stigmas have disappeared. The pedicels in some of the staminate flowers are twice as long as the involucres, and in the fruiting aments vary from once to thrice as long.

This was abundant at Twin Lakes, the head waters of Cañon Creek, Trinity county, and was collected with immature fruit July 10, 1901. A single bush with dried staminate aments was found from which the comparison with the flowers of typical *G. Fremontii* was made.

Garrya salicifolia, sp. nov.— Stems slender, diffusely branched, marked and roughened by the lenticels; younger stems slightly pubescent. Leaves lanceolate, attenuate at each end, thin and coriaceous, veiny, glabrous or with few fine, scattered hairs chiefly on the margins, 3–6^{cm} long, 1–1.5^{cm} wide; petioles slender, 5–10^{mm} long, angled, pubescent. Aments erect in fruit, sparingly branched at base, slender, angled, slightly pubescent; bracts similar to the leaves but much smaller, 5–10^{mm} long, 1–2^{mm} wide. Berries globose, subsessile, generally two to each whorl, tipped when the styles fall away with a roundish, rough cap.

This is no. 259 Brandegee. It was collected at Sierra de la Laguna, Lower California, January 23, 1890. The smooth, willow-like leaves are very characteristic and sufficiently distinguish it from allied species. It is related and nearest to *G. laurifolia* Benth., but that has much larger leaves and differently shaped berries. It also approaches *G. longifolia* Rose, from which it differs in pubescence, foliage, and habit.

My most hearty thanks are due to Dr. B. L. Robinson, of the Gray Herbarium, Mrs. T. S. Brandegee, Mr. H. M. Hall, of the University of California, and Mr. Le Roy Abrams, of Stanford University, for the generous loan of valuable specimens.

BRIEFER ARTICLES.

THE TRANSPIRATION OF SPARTIUM JUNCEUM AND OTHER XEROPHYTIC SHRUBS.

(WITH TWO FIGURES)

IT seems to be somewhat generally taken for granted that shrubs of decidedly xerophilous character, with early deciduous leaves and highly developed green cortex, must depend mainly on the latter for photosynthesis.

Grisebach makes the statement in regard to *Spartium junceum* L.: "At certain seasons this shrub develops little isolated leaves; these are of no physiological value whatever."[1] Kerner says of the leaves of the same shrub: "But these are of such secondary importance that their green tissue can form only the smallest portion of the organic substances necessary to the further growth of the plant, and this duty chiefly falls to the share of the cortex of the switch-like branches."[2] Other authors are less explicit in regard to the uselessness of the leaves of Spartium, but dwell much on the activity of the cortex.

Without more apparatus than was at my command it was not possible for me to investigate the relative amount of photosynthetic work done by the leaves and the cortex respectively. But it was a comparatively easy matter to ascertain the relative amount of transpiration accomplished by the leaves and by the cortex of the slender branches and twigs.

Young vigorous branches were taken and compared, two by two, until a pair of almost precisely equal area of cortex were obtained. This was not a difficult matter, as the form of all the branches is so nearly alike. One branch was then stripped of its leaves, and the scars left by their removal covered with melted beeswax, to which 5 or 10 per cent. of olive oil had been added, to lower the melting point. The freshly cut, larger ends of the branches were then submerged in water in test-tubes, which were fitted with corks, each with a double perforation, to admit the branch and a capillary tube for air to supply the

[1] GRISEBACH, Die Vegetation der Erde, Tchihatchef's French translation, 1: 411. Paris. 1877. The German original is not to be had in Naples.

[2] KERNER, Pflanzenleben, Oliver's translation, 1: 330. N. Y. 1895.

place of absorbed water. Tube and branch were then sealed into the cork with the beeswax mixture, and the leafy and the leafless branch thus arranged were placed out of doors for some hours in full sunshine, after being carefully weighed. Reweighing at the end of the period gave the loss of water.

On April 5 the leaves had not attained their full size, but nearly so, and were in excellent condition for the experiment. A branch 40^{cm} long had twenty-three leaves, with a total area (reckoning one surface only) of 17.5^{sqcm}. The area of the branch with its four twigs, was about 51.8^{sqcm}.

In three hours of sunshine, at a temperature in the shade of 20 to 22° C., the leafless branch lost 1.32^{gm} water and the leafy one 2.47^{gm}. The probable loss of water through the leaves of the leafy branch was therefore $2.47 - 1.32$ or 1.15^{gm}. Ratio of $\frac{\text{loss by leaves}}{\text{loss by stems}} = \frac{1.15}{1.32} = 0.87$. The ratio of the loss by unit area of the leaves to that by unit area of the stems would therefore have been about 0.87×3 or 2.61. It should be noted, however, that the upper epidermis of the leaves of Spartium contains a good many stomata and doubtless performs a considerable part of the work of transpiration, so that the value 2.61 is somewhat too large.

A repetition of the experiment on April 13, when the leaves had practically attained their full size (except in the case of a few at the tips of the branches), gave a loss of 3.24^{gm} for the leafy branch and 1.15^{gm} for the leafless one. The branches were for three hours in full sunlight at a temperature of 22° C. during most of the experiment.

The relative amount of transpiration performed by the leaves and the green cortex of this shrub is evidently not necessarily a measure of the relative amount of photosynthetic work. But it would seem probable that, since the leaves excrete a much larger amount of watery vapor in proportion to their area than the cortex does (and sometimes a larger total amount), they must also fix more of the carbon dioxid admitted to the tissues of this plant than the cortex does.

Some indirect evidence points very strongly in the same direction. Most of the growth of the Spartium in the neighborhood of Naples takes place between February 1 and July 1. I have no detailed numerical statement to make on this head, since the idea of taking measurements for the purpose did not occur to me until too late in the season. But two years' observation has made me sure of the fact above stated. Leafy individuals examined June 1 show branches 50^{cm} long

which have reached these dimensions since February. The leaves of the shrub first appear in considerable numbers about February 1, and they begin to turn yellow, preparatory to falling, about June 1. During the comparatively rainless period from late June until late September, the growth of the leafless shrub is extremely slight, and its obvious activity is almost wholly in the direction of growing and ripening the fruit.

In corroboration of the view that the photosynthetic work of this

FIG. 1.—Part of a leafless shrub of Spartium, photographed July 1. It has borne no leaves for a year, but has blossomed and is fruiting.

FIG. 2.—Part of a leafy shrub of Spartium, photographed July 1. The leaves are on the point of falling. It has borne hardly any flowers or fruits.

plant is done largely in the leaves, may be given the additional fact that some individuals produce no leaves or hardly any during certain years. Whether there is any alternation of leaf producing and leafless years for the same individual, I do not know. Now the leafless plants, at the end of May and beginning of June, when their neighbors are in full leaf and growing with great rapidity, are found to have made hardly any growth during the entire spring. But the leafless specimens often bear many flowers, and the leafy ones are comparatively flowerless. A glance at the accompanying figures will give some idea of the relative appearance of the two sorts of shrubs.

Time has not permitted the examination of the amount of transpiration accomplished by the leaves of the whole number of summer deciduous shrubs which occur in this region. Two of the most important species are *Calycotome villosa* Link and *Cytisus scoparius* Link. The former ot these gave on two successive days, with different specimens each day 2.6 times and 3.3 times as much loss from leafy as from leafless branches. The latter on different days and with different specimens gave 3.5 times and 3.1 times. These experiments were conducted exactly like those with Spartium.

My conclusions may be briefly summarized as follows:

1. In the three species examined, *during the leafy season*, the relative power of transpiration of the leaves as compared with that of the cortex is much greater, for equal areas.

2. During the leafy season, the total transpiration due to leaves may be more than three times as great as that due to cortex.

3. Photosynthetic work due to leaves is probably much greater during the leafy season and perhaps for the entire year than that due to cortex.

4. Leafless individuals of Spartium grow but little at any season.—JOSEPH Y. BERGEN, *Naples, Italy*.

GEASTER LEPTOSPERMUS: A CORRECTION.

IN the number of the BOTANICAL GAZETTE for October last, page 306, in the technical description of *Geaster loptospermus* Atk. & Coker, n. sp., occurs a typographical error in lines 14 and 22, the μ being used in place of mm. The measurements in these lines should read 3–4.5^{mm} and 2.5–3.5^{mm}. In the general text the measurements were properly given, the error occurring only in the technical description.—GEO. F. ATKINSON, *Cornell University*.

CURRENT LITERATURE.

BOOK REVIEWS.

The Bonn text-book.

THE SECOND ENGLISH EDITION of the translation of what has come to be called familiarly the "Bonn" text-book — Strasburger, Noll, Schenck and Schimper's *Lehrbuch der Botanik* — has been revised to conform to the many changes in the fifth edition of the original work.[1] No other general text-book of botany has yet appeared that seems so nearly to meet the requirements of the university student. There is little evidence that the text was not originally written in English, and yet the style and characteristics of the original have not been lost in translating. The plan of the work, its main divisions into general and special morphology and physiology are the same as in the earlier editions, but the arrangement of the special topics has been made much more logical. Chapters have been recast and several entirely rewritten, either to incorporate recent investigations or to eliminate errors. In many instances original illustrations or reproductions from late monographs have replaced unsatisfactory figures. This is particularly true in the chapter which treats of cell division. The drawing of a typical vegetative cell (p. 51) which takes the place of the well-known figure with its bullet-like centrospheres, is much less likely to strain the student's credulity than its predecessor. There are helpful suggestions as to the selection of illustrative material, and of great value are the references in the text to the index of important literature on the special topics under discussion. The introduction, which is a succinct statement of the modern theory of evolution from the botanist's standpoint, has been revised to include DeVries's mutation theory.

From the point of view of the instructor, who often to his regret realizes the influence the printed page has upon the average student, one regrets that in a book of this sort more care should not be taken in the plants chosen for types. *Marchantia polymorpha* as usual is illustrated by several figures giving the important phases of its life history, whereas there are only habit sketches of Anthoceros and a Jungermannia form. It is difficult on this account to persuade a class that Spirogyra, Mucor, and Marchantia are not typical of the algae, fungi, and liverworts respectively.

At the risk of appearing captious, one is inclined to protest against the colored pictures which are so bad from every point of view that they are quite unworthy of a dignified book. Many modern morphologists will

[1] STRASBURGER, E., NOLL, F., SCHENCK, H., and SCHIMPER, A. F. W. A text-book of botany. Translated from the German by H. C. PORTER; 2d edition revised with the 5th German edition by W. H. LANG. 8vo. pp. ix+671. *figs. 686.* New York: Macmillan & Co. 1903. $5.

hardly agree with the statement (p. 158) that "flowers are the organs of sexual reproduction in plants," nor in the light of recent work done in physiological chemistry, can they affirm that "the physical attributes of air, water, and of the gases and metals used in the physical apparatus *can never* explain qualities like nutrition, respiration, growth, irritability, and reproduction." Only a teleologist or a poet would feel justified in saying that a membrane "has the power of decision whether a substance may or may not enter a cell." Occasionally one finds an error that has escaped the proof reader and is misleading. For example (p. 442) the embryo sac is described as "consisting of six cells which are formed in groups of three at each pole." Although these petty criticisms might be multiplied, they are inconsequent and need not be noted when the scope and high quality of the book as a whole is concerned. — FLORENCE M. LYON.

Ferment organisms.

THE TRANSLATION by Allan and Millar of Klöcker's book *Gärungsorganismen* (1900)[2] renders this work accessible to all English-speaking students, and places a valuable text-book in the hands of those interested in the microbiology of fermentation industries. In the discussion of ferment organisms and the history of their relation to industry, two names stand out with especial prominence, those of Pasteur and Hansen. Pasteur's discovery that bacteria were responsible for the diseases of fermented liquids led to the prevention of external infection, but could not be fruitful until Hansen had made practical application of his methods of distinguishing and securing pure yeast-cultures. In any text-book on fermentation organisms the results of investigations in the Carlsberg laboratory must therefore form an important part, and Klöcker, for years the assistant and distinguished associate of Hansen, is especially fitted to present these results.

The book is divided into three sections. The first of these, pp. 1–15, is introductory and historical; the second, pp. 16–169, describes the fittings and methods of a zymo-technical laboratory, with especial attention to the preparation of pure yeast-cultures, to Hansen's methods for preservation of yeasts, for preparation of spore-cultures, for analysis of top and bottom yeasts, and to his pure-culture system as applied to various fermentation industries. The third section, pp. 170–345, gives a brief but excellent systematic description of Eumycetes, including a general discussion of the structure, development, fermentation phenomena, adaptability, variation, and circulation in nature of Saccharomycetes. The text ends with a short description of those fission fungi which are related to alcoholic fermentation. Each section has its separate bibliography, and though this plan necessitates some repetition of titles, the critical and historical notes by the author on the more important works give the lists unusual interest and value.

[2] KLÖCKER A., Fermentation organisms, a laboratory hand-book. Translated from the German by G. E. ALLAN and J. H. MILLAR. 8vo. pp. xx + 392. *figs. 146*. London and New York: Longmans, Green & Co., 1903.

Although, like the briefer work of Jörgensen on the same subject, this book deals particularly with the malting and brewing industries, it will find an important place in many laboratories, both as a complement to the text-books which treat the chemical side of fermentation and as a systematic reference book.—MARY HEFFERAN.

Ferns.

THIS ELEGANT VOLUME [3] is intended primarily for amateurs and consequently is as free as possible from technicalities. An analytical key based upon the stalks is a principal feature of the book. In this key, the number of vascular bundles appearing in a transverse section of the stalk is the most important character. The chief divisions are those in which the cross section shows one, two, three, four, five, and more than five bundles, respectively. Other stem characters, such as the grooves, ridges, and color are prominent. There is also a key based upon the fructification. All the ferns of the northeastern states are figured and described, there being more than three hundred photographs, all of which are original. The photographs of sori, most of which are taken at a magnification of 5.5 diameters, are exceptionally fine and will be valuable not only to the amateur who is learning to identify ferns, but also to the teacher, who will find them useful in demonstration. In photographing the sori, a camera with a bellows extension of twenty-four inches was used, and the focal length of the lens was reduced by slipping over it a cheap copying and enlarging lens, thus giving the desired magnification.

While the book is addressed to amateurs and is written in popular style the author's acquaintance with ferns in the field, together with the peculiar key and excellent illustrations, will make it useful to the experienced botanist.—C. J. CHAMBERLAIN.

MINOR NOTICES.

PART 17 of Engler's *Das Pflanzenreich*, a volume of 326 pages, treats the Lythraceae by E. Koehne.[4]

GREEN[5] has revised his *Forestry in Minnesota*[6] and made it more applicable for general use. A very valuable part of the volume is a tabular classification of what is known of the sylvicultural habit and uses of the

[3] WATERS, CAMPBELL E., Ferns, a manual for the northeastern states, with analytical keys based on the stalks and on the fructification. 8vo. pp. ix+362. Illustrated, New York: Henry Holt & Co. 1903. $3.

[4] ENGLER, A., Das Pflanzenreich. Regni vegetabilis conspectus. Heft 17. Lythraceae: E. Koehne. 8vo. pp. 326. *figs.* 59. Leipzig: Wilhelm Engelmann. 1903. *M* 16.40.

[5] GREEN, H. C., Principles of American forestry. 12 mo. pp. xiii + 334. *figs.* 73. New York: John Wiley & Sons. 1903. $1.50.

[6] BOT. GAZ. **34**: 455. 1902.

important American timber trees. This will be much appreciated by students of forestry.—H. N. WHITFORD.

IN A VERY attractive volume Snow[7] discusses the species and properties of a large number of native and foreign species of wood. A valuable feature of the book is the half-tone reproduction of photographs of trees, bark, and wood of many species, usually one plate for each genus that is treated. The work is an untechnical presentation of the subject. It would have been wise to substitute modern terms for "exogenous" and "endogenous" in the text. —H. N. WHITFORD.

NOTES FOR STUDENTS.

SCHMIED reports[8] a carotin dissolved in oil in the periderm of the roots of *Dracaena reflexa*, which is identical in many respects (not in all), with the carotin of Dancus.

IN A WORKING PLAN for some forest lands in South Carolina Sherrard[9] gives data concerning the silvicultural habits of the southern pines in this state.—H. N. WHITFORD.

SCHWARZ[10] thinks the diminished flow of the Rock River is due to the deforestation of large tracts of land in its basin. Cultivated lands and wood lots have been largely converted to pasturage, thus interfering with waterflow. He advises a more careful treatment of the present forest and its enlargement where it will not interfere with land more valuable for agricultural purposes.— H. N. WHITFORD.

CHARPENTIER[11] finds that the green alga, *Cystococcus humicola*, grows luxuriantly in solutions, the air above which is lacking in CO_2. The necessary carbon in such cases may be taken from glucose. The green color may develop in the dark, though growth is less rapid in this condition. When required to depend upon atmospheric CO_2 as a source of carbon, the growth of Cystococcus is very slow.—H. C. COWLES.

A REPORT of the Bureau of Forestry of the Philippine Islands[12] contains

[7] SNOW, H. C. The principal species of wood; their characteristic properties. 8vo. pp. xi + 203. *pls. 39. figs. 4.* New York: John Wiley & Son. 1903. $3.50.

[8] SCHMIED, H., Ueber Carotin in den Wurzeln von Dracaena und anderen Liliaceen Oesterr. bot. Zeits. **53**: 313–317. 1903.

[9] SHERRARD, T. H., A working plan for forest lands in Hampton and Beaufort counties, South Carolina. Bull. no. 43, Bureau of Forestry, U. S. Dept. of Agric. pp. 54. *pls. 12. figs. 11. 1 map.* 1903.

[10] SCHWARZ, G. F., The diminished flow of the Rock River in Wisconsin and Illinois, and its relation to the surrounding forests. Bull. no. 44, Bureau of Forestry, U. S. Dept. of Agric. pp. 27. *pls. 6. 2 maps.* 1903.

[11] CHARPENTIER, P. G., Sur l'assimilation du carbone par une algue vertue. Compt. Rend. **134**: 671–673. 1902.

[12] REPORT of the Bureau of Forestry of the Philippine Islands from July 1, 1901, to September 1902. pp. 451–527. Report of the Philippine Commission.

some interesting matter concerning the condition of forestry there. There are between 600 and 700 native arboreal species of which there is some information, but there is great confusion in both scientific and popular names. Considerable work has already been done in ascertaining the condition of the forests in various parts of the Island.—H. N. WHITFORD.

ALEX. ARTARI, has been studying the relation of chlorophyll to light in some algae, especially Stichococcus.[13] The development of chlorophyll in the dark is possible only when the nutrition is good. Similarly chlorophyll often vanishes in the light under highly favorable nutrition conditions. Artari thinks that the disappearance of chlorophyll in the phylogenetic development of parasites is thus a matter of nutrition and bears no relation to light. —H. C. COWLES.

NĚMEC[14] has compressed the growing apices of shoots of *Nepeta macrantha*, and studied the effects on the leaf primordia. By preventing the growth of one the position of these is usually modified but in one experiment the phyllogenous tissue was extended beyond the normal. As was expected, the number of rows of leaves was not modified. It may be remembered that Vöchting found the number of rows of leaves of some cacti dependent on the illumination and changeable with it.—E. B. COPELAND.

V. KINDERMANN[15] has confirmed the results of Leitgeb and Molisch as to the resistance of guard cells, and added new data. Many agents were employed, such as acids, alkalis, harmful vapors, illuminating gas, desiccation, lack of oxygen, and in every case guard cells are found to be more resistant than other cells. They sometimes remain alive for several days after the death of other leaf cells. The author thinks this resistance is not referable to the cell wall, but is a property of the cytoplasm.—H. C. COWLES.

ED. GRIFFON, whose previous studies on chlorophyll are well known, has reinvestigated some of Boussingault's results,[16] from which it has been commonly supposed that the synthetic power of the palisade cells far exceeded that of the spongy parenchyma in ordinary leaves. The earlier results are confirmed in a general way, though the difference is much less than Boussingault thought. The maximum difference in favor of the palisade was found to show the ratio of 100 to 54 instead of Boussingault's 6 to 1. The ratio is

[13] ARTARI, ALEX., Ueber die Bildung des Chlorophylls durch grüne Algen. Ber. Deutsch. Bot. Ges. **20**: 201–207. 1902.

[14] NĚMEC, B., Ueber den Einfluss der mechanischen Factoren auf die Blattstellung. Bull. Internat. Acad. Sci. Boheme. 1903, pp. 14.

[15] KINDERMANN, V., Über die auffallende Widerstandskraft der Schliesszellen gegen schädliche Einflüsse. Sitzb. Akad. Wiss. Wien. Math.-Nat. Classe, Abth. I, III: 490–509. 1902.

[16] GRIFFON, ED., Recherches sur l'assimilation chlorophyllienne des feuilles dont on éclaire soit la face supérieure, soit la face inférieure. Compt. Rend. **135**: 303–305. 1902.

100 to 92 in the almost homogeneous mesophyll of the bamboo leaf.—H. C. COWLES.

THE EMBRYO-SAC of two sterile hybrids is discussed in a recent paper by Tischler.[17] The hybrids are *Ribes Gordonianum* Lem. (*R. aureum* × *sanguineum*) and *Syringa chinensis* (*S. vulgaris* × *persica*). Both parents of *R. Gordonianum* have normal embryo sacs with conspicuous nutritive tissue in the chalazal region of the ovule. In the hybrid this nutritive tissue is lacking and the development of the embryo sac is usually checked long before it reaches the fertilization period, the megaspores often failing to germinate at all.

In the parents of *Syringa chinensis* the nutritive tissue is in the form of a jacket derived from the integument and surrounding the embryo sac, which in both cases is normally developed. In the hybrid the nutritive jacket is more highly developed than in the parents, but the embryo sac becomes disorganized quite early, so that the stage at which fertilization might occur is seldom or never reached.

References are given to the few cases previously described of irregularities and imperfections in the development of the ovules and embryo sacs of sterile hybrids.—C. J. CHAMBERLAIN.

P. D. BUCK [18] has made a comprehensive study of the stomata and aeration tissues of a large number of Swiss plants, especially those of beech woods. A number of modifications of Schwendener's types are described, together with a new type, that of *Ranunculus acer*. Buck describes a number of variations on the same individual, especially differences in the level of the guard cells. While some groups, such as conifers, sedges, and grasses, are characterized by a definite structural type, it is more common to find rather a relation to the form of the leaf, or to the habitat. Perhaps his most interesting contribution deals with subterranean stomata, of which he finds three types: functional, functionless, and latent. The latent stomata attain full development only when the shoot which bears them comes above the surface. For the functional subterranean stomata, Mohl's theory as to the mechanism, of course, cannot be held, as there is no chlorophyll or synthetic activity, though starch is present. They were found to open and close like ordinary stomata when the moisture content of the air was changed. The last section of the paper deals with the spongy parenchyma, of which several types are noted.—H. C. COWLES.

THE U. S. Bureau of Soils in a recent bulletin [19] presents a comprehensive study of the influence of soil chemistry upon crop production. It is shown

[17] TISCHLER, G., Ueber Embryosack-obliteration bei Bastardpflanzen. Beih. Bot. Centralbl. **15**: 408–420. *pl. 5*. 1903.

[18] BUCK, P. D. Beiträge zur vergleichenden Anatomie des Durchlüftungssystems. Inaugural Dissertation. Freiburg i. d. Schw. 1902. pp. 93.

[19] WHITNEY MILTON, and CAMERON, F. K., The chemistry of the soil as related to crop production. Bull. 22, Bureau of Soils. U. S. Dept. of Agric. pp. 71. 1903.

that in practically all cultivable lands no such influence exists. The soil water is at all times nearly saturated with the difficultly soluble minerals of which the soil is composed, and several hundred analyses of water from soils of every type and degree of fertility showed in almost every case that the materials essential for the plant are present in considerable excess of the amount required for the production of good crops. This result agrees well with the observations of students of physiographic ecology, that the chemical composition of the underlying rocks is of little significance in determining the development of vegetation, and it furnishes a sound basis for the explanation of this observed fact. It also emphasizes the importance of the study of soil physics, since it is in the physical properties of the soil that we must find the explanation of the important influences of soil upon vegetation. There are brief chapters upon the influence of climate, of texture of the soil, and rotation upon the yield of crops, and upon the rôle of commercial fertilizers. In an appendix is a concise description of the methods used for the quantitative determination of the various ingredients of soil waters. This will be greatly appreciated because of the simplicity of the apparatus, the ease of manipulation and the accuracy of the results.—G. H. SHULL.

IN THE RUST, *Coleosporium sonchi-arvensis* Lév.[20] during certain stages in the life history the cells contain two nuclei and at other stages but one nucleus. The uredospore and the cells of the mycelium to which it gives rise, contain two nuclei which divide by conjugate division, *i. e.*, each nucleus contributes to each of the two daughter-cells. The teleutospore produced from this mycelium is the last binucleate cell of the series. The two nuclei of the teleutospore fuse, after which the teleutospore at once germinates into a four-celled promycelium, each cell of which contains but a single nucleus. Each of the four-cells of the promycelium produces a uninucleate sporidium. The first division of the nucleus of the sporidium is not followed by cell division, but starting with the sporidium there is developed a mycelium of binucleate cells. In short, from teleutospore to sporidium the cells are uninucleate, and from sporidum to teleutospore, binucleate.

The two nuclei which fuse in the teleutospore have maintained a separate existence throughout almost the entire life cycle of the host, and there is some evidence that the chromosomes, in the division of the fusion nucleus, are collected into two groups representing, possibly, the chromosomes of the male and female nuclei. While there is no proper cell fusion, the union of nuclei more or less separated in origin is not out of harmony with our conception of sexual reproduction in other groups of plants.—C. J. CHAMBERLAIN.

RUHLAND has presented in full[21] the results of his studies on several of

[20] HOLDEN, R. J. and HARPER, R. A., Nuclear divisions and nuclear fusion in *Coleosporium sonchi-arvensis* Lév. Trans. Wis. Acad. Sci. **14**: 63–82. *pls. 1–2.* 1903.

[21] RUHLAND, W. VON, Studien über die Befruchtung der *Albugo Lepigoni* und einige Peronosporeen. Jarhb. Wiss. Bot. **39**: 135–166. *pls. 2.* 1903.

the Peronosporales.[22] *Albugo Lepigoni* is near the level of *A. candida* in the interesting series of species in this genus, or if anything, more highly specialized, chiefly on account of its extraordinarily large and well differentiated coenocentrum. Ruhland agrees with Berlese and Wager that *Peronospora Alsinearum* has a uninucleate egg and well differentiated coenocentrum; and with Stevens that there is in *Sclerospora graminicola* a rather vague area of denser protoplasm in the center of the egg in place of a clearly defined coenocentrum, though otherwise it is very much like Peronospora. *Plasmopara densa* entirely lacks a coenocentrum and therein differs from *Plasmopara alpina* as recently described by Rosenberg. Ruhland observed a specimen of Plasmopara in which two mature oospores and a younger egg lay side by side, making three differentiated regions of ooplasm in the same oogonium. Such conditions might prove very interesting if one could follow the developmental history.

Ruhland discusses a number of the topics which the reviewer has recently treated in his paper on Saprolegnia. He agrees that the uninucleate egg in the Peronosporales is at a higher level of sexual differentiation than the multinucleate; criticises Trow's comparison of the coenocentrum to a "whirlpool in a river;" holds that the nuclear divisions in the oogonium are not established as reduction divisions; and is not willing to accept Rosenberg's recent comparison of these mitoses to the divisions in the spore mother-cell. —B. M. Davis.

A discussion has arisen over the characters of the genus Monascus. Ikeno[23] calls in question the identity of the form whose ascocarp has been recently described by Barker.[24] Monascus has formerly always been included among the Hemiasci. Barker found in his type a curious but nevertheless well-established system of ascogenous hyphae developing from the fertilized ascogonium, which clearly removes this form from the Hemiasci and so confident was Barker of its identity with other material of the same name that he regarded the entire genus as true Ascomycetes. Ikeno is not able to find ascogenous hyphae in the form which he considers *Monascus purpureus*. The ascogonium develops directly into a large cell, which becomes loosely invested by surrounding hyphae, and the spores arise by free cell formation within this—processes typical of the Hemiasci. Ikeno then holds to the old characters of Monascus and regards Barker's form as entirely distinct from this genus and a typical ascomycete. It is unfortunate that Ikeno does not present a full account of the period when the fertilization of the ascogonium should be expected and the stages of development immediately following this event. This is exactly the time when ascogenous

[22] See notice of preliminary paper, Bot. Gaz. **35**: 221. 1903.

[23] Ikeno, S., Ueber die Sporenbildung und systematische Stellung von *Monascus purpureus* Went. Ber. Deutsch. Bot. Gesells. **21**: 259–269. 1903.

[24] Ann. Botany **17**: 167. 1903.

hyphae, if present, would be most easily found. As Barker states, there is little trace of their presence in later stages when the spores are formed. The account of Ikeno is, however, very positive as to the entire absence of ascogenous hyphae, and it is hard to see any place for them in the series of figures that he presents. Barker and Ikeno must either have had very different organisms, or there is a slip somewhere in one of the accounts of these authors.— B. M. DAVIS.

OLIVER[25] characterizes the Paleozoic gymnospermous seeds by the importance and dimensions of the pollen chamber and the complicated vascular system which embraces the body of the nucellus. He considers chiefly the cordaitean genus Stephanospermum, representing Brongiart's Radiosperms, and Cardiocarpus representing the same author's Platysperms, both from the French Permo-carboniferous. The latter possess many cycadean features, such as the relatively small pollen chamber and the thickening of the cells of the beak of the nucellus. They are more archaic, however, than the former. While paleobotanical terminology denominates these remains "seeds," they are usually preserved at a stage just preceding fertilization, and therefore answer to the modern unfertilized ovules. He next considers the genus Lagenostoma from the Lower Coal-measures of Lancashire and Yorkshire, chiefly as exemplified by *Lagenostoma ovoides* of Williamson. It is small and circular, and has a chambered apex with vascular prolongations which are quite unique. It resembles Cycads in the considerable area of "fusion" between the nucellus and testa, as well as in the presence of vascular strands in the plane of fusion. The confined form of the pollen chamber marks an advance in precision on the open type of the ordinary Paleozoic seeds. Modern cycadean structures are considered, as shown in *Cycas Rumphii*, and the paper closes with an examination of the modern species of Torreya, which, though siphonogamous as in all other conifers, still retains marked traces of the fertilizing contrivances that became obsolete when siphonogamy appeared.

Oliver also records[26] the discovery that the *Sporocarpon ornatum* of Williamson is really a transverse section of *Lagenostoma physoides* of the same author.

He also notes[27] a fungus on the fronds of Alethopteris from the Stephanian of Grand Croix, and of chytridineous sporangia in the nucellus layers of Sphaerospermum from the same formation.— E. W. BERRY.

VARIATION in the number of stamens of *Alsine media* L. has been studied during several years by Reinöhl,[28] using a combination of the statistical and

[25] OLIVER, F. W., The ovules of the older gymnosperms. Annals of Botany **17**: 451–476. *pl. 24, fig. 20.* 1903.

[26] OLIVER, F. W., New Phytologist **2**: 18. 1903.

[27] OLIVER, F. W., New Phytologist **2**: 49. 1903.

[28] REINÖHL, FRIEDRICH, Die Variation im Andröcium der *Stellaria media* Cyr. Bot. Zeit. **61**[1]: 159–200. *pls. 2–4.* 1903.

experimental methods. Field studies showed that the stamens vary from 0 to 13, forming a bimodal curve with principal maximum on 3 and secondary maximum on 5. The relative prominence of the maxima, the value of the mean, and the coefficient of variability depend upon habitat and time at which collections are made. Although in nature the curve was always bimodal, three of the cultures produced asymmetrical monomodal curves which agreed with Pearson's theoretical type IV, in one instance the asymmetry being so slight as to give essentially the Gaussian probable error curve. This reduction to a homogeneous condition is an unusual result where the homotyposis of organs which have their origin in relation to the phyllotactic spiral is involved. The maximum on 5 was found to be completely eliminated in the third generation of plants grown in diffused light, while that on 3 was eliminated by the high manuring of plants which had been observed to have already a strong development of the higher mode. By still higher manuring he secured a curve with a strong maximum on 5 and a slight one on 8, showing thus by the maxima on 3, 5, 8, a perfect agreement with the Schimper-Braun series. Of the external factors light intensity was found to be the most important, and the richness of the soil in available foods next.

Finally it was found that in all cases the modal condition changes as the flowering season advances, the number of stamens beginning low, reaching its maximum only after some time, and falling again near the end of the season. This contravenes Burkill's[29] conclusions, which rest upon occasional collections aggregating less than 400 flowers cultivated in pots in a tropical greenhouse, while Reinöhl has observed 44,542 flowers, including in the case of cultures all the flowers produced during the flowering season. It also differs from observations by the reviewer[30] on *Aster prenanthoides* Muhl., the reason probably being that in *Alsine media* the height of vegetative activity is not reached until some time after the flowers begin to bloom, while in *Aster prenanthoides* the maximum vegetative activity precedes the development of the flowers.—G. H. SHULL.

E. HEINRICHER'S studies of the green half-parasites[31] have advanced considerably the boundaries of our knowledge. It was to have been expected that a group like the Rhinanthaceae, apparently half way on the road to holoparasitism, would yield results of surpassing interest. In his earlier paper Heinricher presents studies on *Odontites Odontites*, *Euphrasia stricta*, and *Orthantha lutea*. He finds that germination is independent of host stimuli, but that haustoria require a host stimulus in order to induce development. Odontites was brought to a state of flower and fruit entirely without parasitic nutrition, while Euphrasia could nourish itself to a much less degree.

[29] BURKILL, On some variations in the number of stamens and carpels. Jour. Linn. Soc. Bot. **31**: 220 *et seq.* 1895.

[30] SHULL, G. H., Amer. Naturalist **36**: 111–152. 1902.

[31] HEINRICHER, EMIL, Die Grünen Halbschmarotzer. Jahrb. Wiss. Bot. **31**: 77–124. 1898; **32**: 389–452. 1898; **36**: 665-752. 1901; **37**: 264–337. 1902.

Any species grows better in dense cultures than alone, showing that stronger individuals grow parasitically upon the weaker. Still stronger individuals result when the normal host plants are supplied. The species which have the greatest autophytic power have abundant root hairs, while the more fully parasitic forms are without them.

In his second paper Heinricher showed that the Rhinanthaceae require light for their development even more than they require a host. Synthesis of carbohydrates was shown by Sachs's iodin test. Various species of Euphrasia differ widely as to their parasitism, some being as independent as Odontites, while some absolutely require a host for full development. His third paper dealt with Bartschia and Tozzia, the forms which come nearest to holoparasitism. In Bartschia haustoria appear in the seedling stage, there are no root hairs, and a bud for the second growth period does not appear unless a host is supplied. Tozzia is the most remarkable form of all. It requires the stimulus furnished by a host root even for germination, differing in this from all other Rhinanthaceae and agreeing with holoparasites like Orobanche and Lathraea. For more than a year the plant lives wholly underground as a holoparasite, while late in the second season a tiny green shoot appears which soon flowers and fruits. Even this plant was shown to have some photosynthetic activity, though less than in any other member of the family. Bonnier found no active photosynthesis in these plants, and more recent authors have been inclined to doubt Heinricher's results. Apparently Heinricher has clinched his case by employing cut shoots and finding synthesis to take place there, although he uses the iodin test rather than the more accurate method of gas determination.

In his last paper Heinricher shows that chlorosis depends upon the lack of iron in the seed, not upon the more complete parasitism of the individual in question, as he at first supposed. In other respects, also, he finds differences in the properties of seeds in the same species, showing that all of one species do not have the same hereditary characters. Wide individual variations are also found to be due to differences of habitat. Strong host plants, for example, permit a better development of parasites. Heinricher is inclined to explain a number of Wettstein's species, especially his aestival and autumnal species, as true habitat variations. As might be expected, this view has called forth a series of polemics[32] which need not be mentioned further.

Heinricher's work gives us a basis for theorizing as to the origin of parasitism, since we find every step in the series within one group of plants. Apparently root hairs are soon lost, the first demand on the host being for raw materials rather than for organized foods. Further parasitism is acquired by drawing upon these organized foods, a process which is ultimately followed by the loss of chlorophyll and photosynthetic power.—H. C. COWLES.

[32] Jahrb. Wiss. Bot. **37**: 685–697. 1902; **38**: 667–688. 1903. Also Oesterr. Bot. Zeits. **52**: 246–249. 1902; **53**: 205–223. 1903.

NEWS.

DR. E. ULE has returned to Berlin with rich collections from South America.

DR. EUGENE ASKENASY, honorary professor of plant physiology in the University of Heidelberg, died recently.

THE *Revue Générale des Sciences* for October 30 contains a full account of the life and work of the late Professor Cornu.

DR. ANTON HANSGIRG, of Prag, has retired after forty years' service as professor of botany in the Imperial University of Bohemia.

DR. E. B. COPELAND has been appointed "systematic botanist" by the Philippine Commission, and sailed November 10 for Manila.

AMERICAN GARDENING announces that Mrs. Phoebe Hearst has provided funds for the erection of a building for the department of botany in the University of California.

THE ROYAL SOCIETY has awarded a medal to Mr. Horace T. Brown for the work on the chemistry of carbohydrates and on the assimilation of carbon dioxid by green plants.

THE LONG PROMISED English translation of Schimper's *Plant Geography*, by W. R. Fisher, revised and edited by Percy Groom and Isaac Bayley Balfour, is promised for December 15 by the Oxford University Press.

DR. ARNOLD DODEL has retired from the professorship of botany in the University of Zürich. The post vacated will not be filled, but Dr. Alfred Ernst, the assistant, will give instruction in general botany and physiology.

AFTER A short illness the well known systematist, Hofrath Professor C. Haussknecht, died in Weimar on July 7. His large herbarium will be maintained by the family under the auspices of the Thuringian Botanical Society.

ON OCTOBER 25, the twenty-fifth anniversary of Professor Hugo DeVries' appointment as professor of botany at Amsterdam, Professor Went, on behalf of his Dutch friends, presented him with 4250 gulden to be devoted to the further study of mutation.

UPON INVITATION the Botanists of the Central States will meet at St. Louis during the annual meeting of the A. A. A. S., December 28, 1903, to January 2, 1904. A business meeting of the society will be held on the morning of December 30, at a place and hour to be announced on the general program.

ACTIVE STEPS are being taken by the Committee of Organization for the international botanical congress at Vienna in 1905 to provide for the discussion, among others, of the nomenclature question, to which the afternoons of the week, June 12–18, are to be devoted. A circular stating the present arrangements has just been distributed, which can be obtained by any who are interested and have not received it by addressing Dr. A. Zahlbruckner, Wien I, Burgring 7, Austria.

HOWELL'S *Flora of Northwest America*, which has been in course of publication since 1897 is now completed. The author has struggled against many difficulties in producing this work, for which he himself has set the type. Those who have used the parts in the field have found it exceedingly useful. The collections of Mr. Howell, containing types of many species, have been acquired by the University of Oregon and he is to be employed in arranging them for use and safe keeping.

THERE IS contained in *Nature* for November 5 an account of the botany at the Southport meeting of the British Association. One morning was devoted to a discussion of heredity, and another to the origin of monocotyledons by the Misses Sargant and Thomas. Professor Farmer gave a semi-popular lecture on stimulus and mechanism. Short abstracts of a number of papers are given. Several botanical excursions were made, especially to the neighboring sand dunes. In the section for Geography there were several papers of botanical interest dealing with plant geography.

THE Society for Horticultural Science was organized September 9, 1903, in the rooms of the Massachusetts Horticultural Society in Boston on the occasion of the twenty-eighth biennial session of the American Pomological Society. The officers are: president, L. H. Bailey; vice-presidents, G. B. Brackett, T. V. Munson, E. J. Wickson; secretary-treasurer, S. A. Beach; assistant secretary, V. A. Clark; executive committee, the president, *ex officio*, L. C. Corbett (chairman), W. R. Lazenby, J. C. Whitten, F. A. Waugh. The object of the society is the strengthening of horticultural investigation and teaching on its scientific side and the aiding in the development of horticulture as a science. The society is especially designed to meet the professional and technical requirements of horticultural investigators and teachers. The field of the society is clearly defined and heretofore unoccupied. It lies between that of the popular societies on the one hand and that of the societies for general science on the other, and connects them. The programs are to include, besides papers on original investigations, summary presentation of scientific knowledge on special horticultural topics. Some one topic of general and immediate interest is to be made the central feature of each program and is to be announced in advance. The first meeting with a scientific program will be held at St. Louis in Convocation Week, December 28–January 2 next.

GENERAL INDEX.

The most important classified entries will be found under Contributors, Personals, and Reviews. New names and names of new genera, species, and varieties, are printed in **bold-face type**; synonyms in *italics*.

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